

Memoirs of the

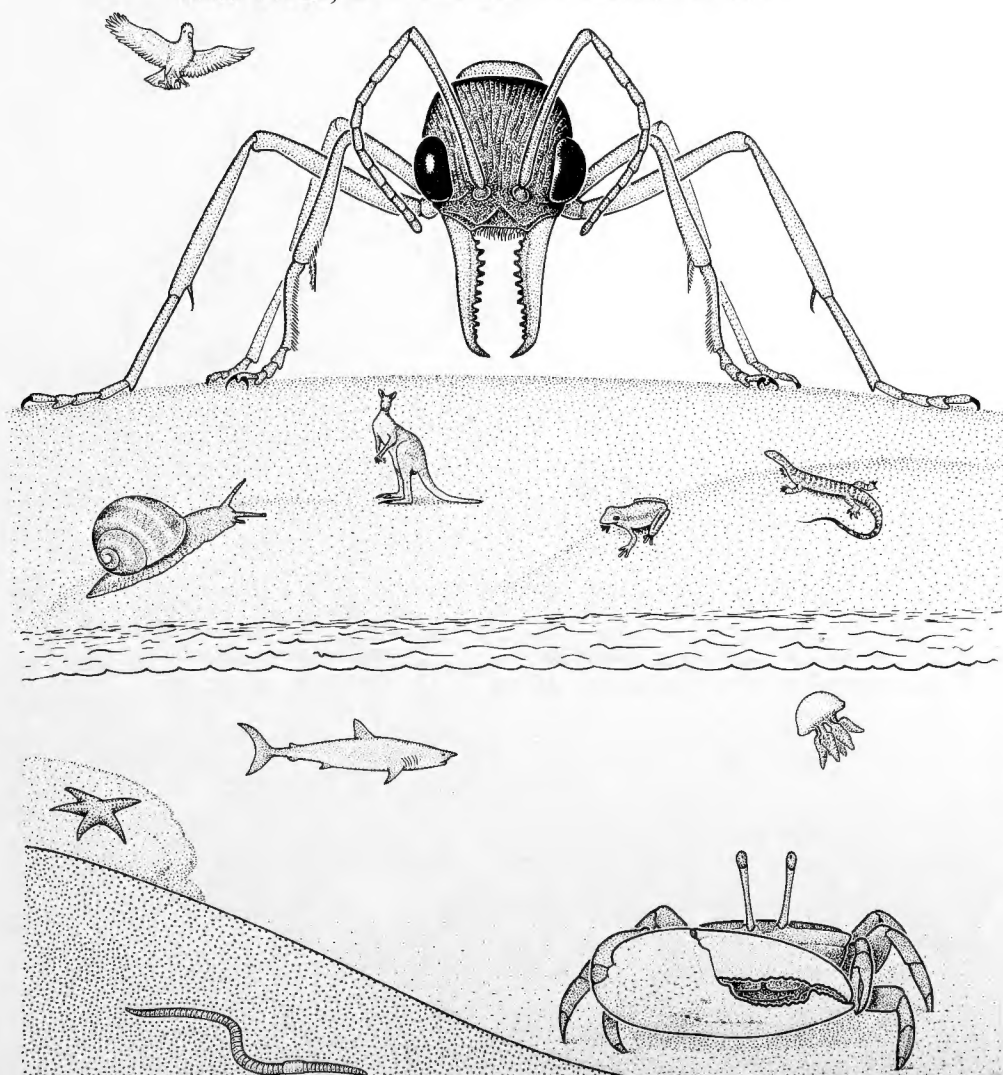
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28 February 1997

Proceedings of the Conference
Invertebrate Biodiversity and Conservation
Melbourne, 27 November–1 December 1995



Cover: The relative abundance of major animal taxa. Illustration by Graham Milledge.

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MUSEUM OF VICTORIA

MELBOURNE AUSTRALIA

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Number 2
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Invertebrate Biodiversity and Conservation
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UNDER THE ICEBERG

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Abstract

Bridgewater, P. and Walton, D.W., 1997. Under the iceberg. *Memoirs of the Museum of Victoria* 56(2): 261–265.

This paper provides a general introduction to the theme of the Conference on Invertebrate Biology and Conservation. The introduction is centred around general consideration of biodiversity patterns and processes, changes to patterns and processes and changes in biodiversity and ecosystem function. Three challenges are posed to biologists who study invertebrates: cooperation among specialists across the taxa; the development of analytical techniques to determine ecosystem/landscape health; and, the presentation of research findings in forms accessible and usable by planners and managers.

Introduction

A small visible portion and the larger submerged portion of icebergs have made the iceberg a familiar simile. Tim New (1995) carried the iceberg allegory further in his latest book on invertebrate conservation. As is the case with the icebergs, much of biodiversity is out of sight. So much, actually, that we can emphasise this by saying that a large portion even is “below the iceberg”. Species and genetic levels immediately come to mind, but there unquestionably are entire communities or ecosystems of micro-organisms, structurally and functionally complete. In most discussions of biodiversity, turbellarians and leeches seldom rate a mention, let alone the denizens of the buccal cavity of a water snake, the fauna of the fur of a sloth or the temporary denizens on the carcass of a whale, which died and sank at depth. Occasionally, we remember such things as the relationship of termites to the protozoans of their gut. Generally speaking, however, the invertebrates with a public profile are likely to be in one of three categories: well-known pests or parasites, popular food items or those notable for their physical beauty or other distinctive peculiarities. One may fairly say that the knowledge base for the species in these three categories greatly exceeds the knowledge of all other invertebrates.

Patterns and Processes of Biodiversity

Biodiversity exists in time and space. Human perceptions of time and space are best when their characteristics are familiar, i.e., most like our own. Time and space for invertebrates varies greatly. The world of an individual proto-

zoan is vastly different from that of the giant squid, life in the gall bladder of an insectivorous bat differs markedly from that in a tunnel of a fallen, decaying spruce. For invertebrates, space and time involves dimensions and durations of such diversity and complex relationships that patterns seemingly act as if they were whole organisms and processes develop unimaginable pathways. Scale is seemingly a paradoxical jumble.

Ecological terminology so clearly useful and precise for vertebrates becomes vague and imprecise when applied to invertebrates. Biological structures and processes vary almost endlessly among invertebrates. Basic and fundamental biological concepts often are challenged. While biologists are terribly fond of counting almost anything, taxonomists are unalterably fond of describing, naming and revising arrangements of organisms, the sheer number of different kinds of invertebrates, organisational patterns within and among individual populations and communities are of such daunting magnitudes that there is little rational hope that counts, descriptions, naming and revisions will ever be completed — or even if so, then fully useful. Space and time interacting with invertebrates yield phenomena that are of such complexity that the identification of particular trends, cycles or other patterns may not be a realistic goal.

Without doubt, the patterns and processes among invertebrates are of immense intellectual interest. They are, moreover, of great importance to functioning of the complex living systems of which they are part. We have made passing reference to scale, but rate is equally important. Change is continuous, but the diver-

sity of rates among patterns and process of invertebrates is seldom appreciated. The apparent obsession with rare and endangered species, as the key to biodiversity, has obscured those species which are exploding in numbers (individuals and populations) or increasing in geographic distribution. Focus on the rare and endangered almost suggests that the flora and fauna are static displays of nature and that evolution and natural selection have ceased. Nothing could be further from the truth. Resistance to pesticides and drugs, exploitation of new man-made environments, successful new distributions and associations in environments far removed from their original are just some of the easily identifiable indicators of the rates of change among invertebrates.

Another myth, that people are somehow not part of natural systems, that "nature" must be kept safe from human influence, is widespread — and nonsense. People are a biological species. We eat many invertebrate species, we live in a state of tolerance with a wide array of invertebrate species, quite a number of invertebrate species depend upon the various activities of people and some live inside or on the outside of our bodies. These associations have arisen over time and space with great diversity of scale and rate, of pattern and process. As the number of people increase, ever greater alteration of the biosphere will occur and the opportunity for invertebrate evolutionary changes and variations in natural selection are magnified. The need, therefore, for us to understand invertebrate patterns and processes also increases. In addition to the important ecological services such as energy and nutrient recycling, invertebrates are competitors for resources and can be the reservoirs, vectors or agents of disease.

The demands for information on patterns and processes among invertebrate species will increase. The role of traditional invertebrate biologists must reflect the adaptability of their subjects. Taxonomy must be more than description and nomenclature, phylogenetic analyses and technique-driven research. It is not enough to put a face with a name in a kinship pattern determined by a trendy method. As important as this information is, it must be in the larger contexts of patterns and processes. The same applies to those working with invertebrates of agricultural, veterinary and medical importance. Solutions to specific problems will continue to be important, but these solutions must be set in the wider contexts of patterns and processes. Technology can provide assistance, but technology

produces its own special sets of problems. Technology, whether in the form of equipment or techniques (especially genetic manipulation or modification) must be evaluated in the larger contexts of patterns and processes. The current emphasis on biosafety in the discussions of the Convention on Biological Diversity underscore these activities. One may easily become complacent and forget just how dynamic living systems can be.

Alterations to Patterns and Processes

At some point in the future, one may look back upon our present and readily identify trends and cycles of durations and amplitudes which to us are not obvious. While the biosphere is a mix of gradual change over time and cataclysmic alteration, invertebrate life not only has persisted, but evolutionarily elaborated patterns and processes to confront the selection pressures of adversity and opportunity. There is no reason to suspect that the forces of change, gradual or cataclysmic, have abated. Established patterns and processes are being altered.

The human population is now approximately 5.5 billion and there are no indications that the number will decrease. Food, fodder and fibre crops to feed the growing number of people will not be distributed as are the human population and their domesticated animals. If we believe the International Panel on Climate Change (IPCC) on global change then there will be more than the usual run of droughts and floods, frosts and hail, pests and pestilence, but most of all there will continue to be political and social disquiet that interrupts plantings, harvests, transport and financial systems and other aspects of traditional societal structure. Locally adapted strains of crops and domestic livestock will continue to be lost. In the midst of such disaster, few have given thought to the implications for invertebrate patterns and processes. The fauna of cropland soil will change, pests and parasites will find new and different hosts, entire ecosystems built upon human dwellings, stock pens, food stores and the like will disappear and patterns and processes associated with seasonal plantings, harvests, burnings, births, deaths and various cultural activities will alter to greater or lesser degrees. If such social unrest is temporary, little may be lost, but if prolonged or intense then desertification or other major change may be the product.

Even if there is no social unrest, human behaviour looms large as a modifier of patterns and

processes. People alter landscapes and seascapes. Not only do they remove or change vegetation, but land form is changed. Hills and valleys are changed into land with minimum contour. Sediment and nutrient input is increased to coastal embayments. Ruthless fishing techniques destroy whole sub-marine communities, many undescribed or even unknown.

Not only is the diversity of vegetation decreased, but often reduced to huge expanses of a single species bordered and partially invaded by plants that indicate human disturbance. The addition of extra nutrients and the applications of pesticides (weed and insect control primarily) generate enormous changes to patterns and processes. Nutrient levels may target the dominant plants of the area, but the impact of the change in available nutrients is highly non-specific. Few pesticides are highly specific and many non-target species are hit. Some of the so-called down-stream effects of additional nutrients and pesticides are well documented, but the case may be that we do not wish to know about other effects.

People, like any other species, produce waste. In addition to biological waste, however, people produce cultural waste. Within any biological community, there are species which are waste converters. They begin the process of releasing energy and nutrients otherwise bound in waste, the flow of bound energy back through the ecosystem. Many of the species along the energy flow detoxify harmful substances and store others in an inaccessible state. Many of these converters and accumulators early in the recycling of energy and nutrients are invertebrates working alone or in partnerships with plants. Patterns and processes have evolved over time so that these organisms act as part of what can be considered as the immune system of the biosphere. Unfortunately, human waste, biological and cultural, occurs in such quantities, kinds and often in such confined space that the normal patterns and processes not only cannot cope, but are totally destroyed. There is also the probability that the few species capable of tolerating large concentrations of toxic substances may be toxic as well or produce wastes of increased toxicity.

Any discussion of this sort invariably includes reference to global warming, global change or both. Without venturing into the arguments about whether global warming is real, no rational biologist can deny that global change is a reality. Change is ever-present. Long before any "global" influence is a factor, local change

will be the major factor in invertebrate patterns and processes. Landscapes are not simply biological, but bio-cultural entities. Species, especially including people, which interact with the local landscape, shape that landscape. Changes to the local landscape alter that portion of the biosphere. If the change is sufficiently drastic, the usual patterns and processes become dysfunctional. The interaction of various landscapes then is affected. Global change, then, is the aggregate of all local change, a situation where the total change may be greater than the sum of its parts.

Biodiversity Change and Ecosystem Function

Discussions purportedly about conservation often convey the impression that ecosystems never change. Loss or addition of species is taken as failure of the ecosystem. Ecosystems are amazingly resilient. Many seem to have depth in species which are ecologically redundant. Again, change as a continuous process is worth re-emphasising. Communities exist in time and space. While there are indications that certain associations of species have persisted over considerable spans of time, we know very little about brief (our perception of brief) associations or whether what we think of as considerable spans of time represent portions of trends or cycles. While much is made of a supposed "balance of nature" equilibrium or homeostasis, in all probability these represent largely imaginary points about which various patterns and processes oscillate, what one might call the comfort range. Under the more usual circumstances of immigration, emigration and land form change, the ecosystem retains a distinctive character. If, however, the ecosystem suffers massive alteration in composition and land form a chaotic state prevails until fluctuations again become confined to a "comfort" range.

Others, and we, have suggested that new combinations and associations will be the dominant ecological feature of the future. While this may seemingly be a new thing for people, people have lived amid and been the agents of great change. There are examples where functional ecosystems have been destroyed and many examples where what we today think "natural" is the creation of people. Examples include tropical rainforests (in reality managed fruit orchards in Central America), the so-called wilderness of most of our country, and the now recognised cultural landscape of Uluru-Kata Tjuta National Park.

What warrants concern? Never before have people existed in such numbers. Never before has technological development been capable of making changes on such a great scale so rapidly. Never before have people made such demands for space and never has so much been extracted at such a rate from the land, water and sea. Most importantly, virtually all of the demands for space and the extractions have been opportunistic, unplanned forays with little or no thought of the consequences. We deal primarily with the results of accumulated small decisions to satisfy short-term goals. There is perhaps an explanation of the disparity in wealth observed in different populations of people in the inability to recognise and accept the carrying capacity of a region, unrealistic expectations of the benefits of technology with an unwillingness to accept the environmental impacts of technology and the acceptance of another's definition of wealth.

Ecosystem function is intimately bound to the expectations of people. What can be extracted from a system, how much disturbance can a system sustain and what defines a healthy system? We must have the answers to these questions.

Invertebrates and non-vascular plants, as well as those organisms which fall between, lie at the heart of any answer to these three questions. We cannot wait until all invertebrate species are collected, described and named. We badly need analytical systems which allow us to determine the health of ecosystems and their limits. We need to be able to identify usual fluctuations from chaos and not confuse biological change with xenophobia. Much is made of "rapid biodiversity assessment" and "all species inventories". But are these exercises useful or necessary? The answer is probably no. More important is to refine our knowledge of the pattern and process of invertebrates, within the framework of adaptive management.

Australia has experienced invasions of alien species at various time in the past. Certainly, in the more recent past there were different waves of immigration of Aborigines. Two hundred years ago Europeans arrived with cultural baggage that included an array of organisms, the number and variety of which continues to expand. Others have commented in detail on general and specific impacts of this baggage. Suffice to say that established biological patterns and processes have been severely disrupted. New combinations and associations of species have developed and others will most certainly emerge.

There is much ado about introduced invertebrate species and certain of them have been singled out for special attention. Without doubt, some of the introduced species have had devastating effects on established patterns and processes. While control is sometimes a viable and necessary option, one must be circumspect about the hope for success. Not all introduced species become established. Some seem to persist marginally until conditions become optimum for their spread. Other invertebrates have been deliberately introduced in the hope that they will either assist in the retention of existing patterns and processes or that they will aid in the establishment of new patterns and processes. The number and variety of alien species now established in Australia preclude the possibility that their eradication is even remotely possible.

Management issues must focus on the interaction of people with the environment. That is conservation. While vertebrate biologists may have the luxury of focusing on individual species, invertebrate biologists will not share this luxury. Valid and reliable indicators of the health of the invertebrate communities of a landscape must be developed. In fact, the complexity of patterns and processes among invertebrates requires multidisciplinary cooperation.

The wealth of detail which will emerge from research and the evaluation of management programs and plans will be such that those responsible for the development of policies, strategies, programs and their implementation cannot possibly absorb the detail. Data must be converted to information and presented in a readily useable form for managers. Detail of interest to scientists must go into the scientific literature. The historic lack of communication between scientists and managers must be over-come. The re-establishment of communication may be tedious and, at times, frustrating, but it must be done. Invertebrate biologists, therefore, have three significant, but self-evident, tasks before them:

1. they must work together;
2. develop analytical techniques to determine ecosystem/landscape health; and
3. present their findings not only for scientists, but for planners and managers.

This is a formidable challenge. One suspects that one of the first steps will be to make an assessment of the requirements for invertebrate specialists and their employment prospects. Teams of specialists must be formed and appropriate analytical methods devised and evalu-

ated, all in an atmosphere of communication with planners and managers. Only then can we begin to assess our efforts for the conservation of invertebrate species. Lists will give us history. Patterns and processes will tell us whether the systems are healthy.

Reference

- New, T.R., 1995. *Introduction to Invertebrate Conservation Biology*. Oxford University Press: Oxford.

“INDICATOR” TAXA IN INVERTEBRATE BIODIVERSITY ASSESSMENT

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Abstract

Cranston, P.S. and Trueman, J.W.H., 1977. “Indicator” taxa in invertebrate biodiversity assessment. *Memoirs of the Museum of Victoria* 56(2): 267–274.

The concept of indicator taxa, widely used in environmental monitoring, has been adopted in the biodiversity assessment literature. Such a transfer can be misleading: such surrogate measures for biodiversity are referred to better as “predictors” — taxa proposed as correlates of wider biodiversity. Using survey data from a sampling protocol applied to five sites in north-east Tasmania, species diversity of terrestrial arthropods were investigated to assess the prospects for ranking sites in systems that are rich in species with poorly known taxonomy, and that change seasonally and erratically. No significant species-richness correlates were found, suggesting that there can be no generalised application of the concept of indicators of biodiversity.

Introduction

Most biodiversity estimates for terrestrial sites have been based on species counts or estimates of abundance in angiosperms (flowering plants) and vertebrates (mostly birds and mammals, although to a lesser extent reptiles and amphibians). Although conspicuous and relevant in terms of human amenity value, these taxa account for a very small percentage of all the world’s species. Site biodiversity estimates that do not consider invertebrates, not only omit the greatest part of what they purport to measure, but also ignore the major contributors to essential ecosystem processes — “the little things that run the world” (Wilson, 1987).

Whilst there is substantial agreement on their significance, precisely how to include invertebrate taxa in biodiversity estimation and conservation is far from evident. Given the huge diversity, and the variable, but usually poor, taxonomic knowledge of so many invertebrates, Australians particularly have advocated certain rapid biodiversity assessment methods (e.g., Oliver, 1993; Oliver and Beattie, 1994; Beattie and Oliver, 1994). Some aspects of this “pseudotaxonomy” have been critically addressed (e.g. Brower, 1995; Campbell, 1995; Cranston and Hillman, 1992; Hammond, 1994; Trueman and Cranston, this volume). Another suggestion for more rapid assessment might be to identify one or a suite of taxa, amenable to easy sampling and identification, whose diversity predicts the diversity of others. This concept has been referred to as “surrogacy” (e.g., RAC, 1993) or as “indication” (e.g., Noss, 1990; Brown, 1991;

Kremen, 1992; Pearson and Cassola, 1992; Williams and Gaston, 1994; Beccaloni and Gaston, 1994; Weaver, 1995) of biodiversity. However, the poorly tested concept of biodiversity “indication” frequently is conflated (*inter alia* by Kremen et al., 1993; Pearson, 1994) with the firmly-established environmental “indication” (e.g., Holloway and Stork, 1991; Cranston and Hillman, 1992; Johnson, 1995). We adopt Kitching’s (1993) terminology of “predictor set” for any subset which is postulated to act as a “surrogate” for the wider, unsampled, complete set.

If the diversity (taxon richness) of traditionally-measured taxa (angiosperms, vertebrates) were to correlate strongly with invertebrate diversity, then it would be valid to assume that conservation of taxon-rich areas for conventionally-surveyed “predictor sets” would provide an “umbrella” to protect the unsurveyed invertebrates. However, the strength of any correlations has, until recently, rarely been addressed directly, and the few results seem contradictory. Thus, Abbott (1974) found 73% of the variation in insect species was accounted for by the number of plant species but no statistical relationship between insect and bird species of remote southern hemisphere islands. The lepidopteran subfamily Ithomiinae correlated well with total neotropical butterfly diversity (Beccaloni and Gaston, 1994) although correlates of butterflies against other prospective indicators were not tested. In contrast, the studies of Yen (1987), on plant/vertebrate/beetle relationships across 32 sites in Victoria, Australia, and in U.K. of Disney (1986) on insect / plants and of

Prendergast et al. (1993) on certain insect/plant/bird relationships, demonstrated little or no correlations. Problems of scale dependence have been identified by Williams and Gaston (1994), who argued that for vertebrate data the few local correlates fail to coincide at global scale, and Weaver (1995), who sampled higher taxonomic groups of invertebrates.

Following the advocacy of Landres et al. (1988), Noss (1990), Longino (1994) and DEST (1995), amongst others, for verification of biodiversity indicator relationships, we specifically test whether:

1. diversity measures obtained from a single arthropod taxonomic group or groups ("predictors" *sensu* Kitching, 1993) predict the diversity of other diversity measures obtained from a single arthropod taxonomic group or arthropod taxa at the same site; and

2. measures of arthropod diversity are congruent with measures based on a conventional diversity estimator, namely diversity of flowering plants.

Methods

Sites

Five sites (A-E), representing the range of natural vegetation types along a 40 km transect in NE Tasmania, were selected to traverse four major terrestrial ecosystems of the ERIN 30-group regionalisation (Thackway and Cresswell, 1992). Sites established were in wet sclerophyll forest (Site A, 3 km N of Weldborough, 41°10' S, 147°54' E) dry sclerophyll forest (Site B, 20 km E of above, 41°09' S, 148°08' E); coastal heathland (Site C, Eddystone Point, Mount William National Park, 41°00' S, 148°19' E.); periodically inundated heath (Site D, Mount William National Park, 41°02' S, 148°15' E.); buttongrass swamp (Site E, Rattrays Marshes, 41°12' S, 148°10' E.). Three of the sites had associated aquatic systems, streams at A and B, swamp at E; site C had an impermanent dune slack (pool) whilst site D was dry. The five sites are such that any reasonable sampling protocol or biodiversity index should be capable of indicating that there are gross differences amongst them, although this should not be taken to mean the respective conservation values necessarily differ widely.

Sampling design

Ten pitfall traps and two yellow pan traps of standard design were set at each site in each of February, May and August, 1993 (Trueman and Cranston, 1994). Pitfalls were opened for 1 week

and yellow pans for 24 hours on each sampling occasion. In February only, ten small pitfall traps of different design were set and equal-effort vacuum samples were taken. Yellow-pan traps on a black background were set in August for comparison against conventional traps. Leaf litter samples were taken at two forested sites on each sampling occasion, and arthropods extracted from the samples over a 1 week period in Tullgren funnels.

All animals from each sample were extracted and identified to ordinal level (insects) or to phylum or other appropriate category (other arthropods). Specimens were counted, identified to Recognisable Taxonomic Unit (RTU) by project personnel inexperienced in the taxonomic group, prepared as necessary for formal identification, and identified by consultant expert taxonomists where available (see *Acknowledgements*). Specimens are deposited in the Australian National Insect Collection, excepting where provided to taxonomists for their ongoing studies.

Results

The observed numbers of species at each site are listed in Table 1. Odonata, Coleoptera and Diptera comprise only adult insects; Diptera is of observed families, not species. Totals are accumulated over all trapping methods, and therefore are not directly comparable as between the two forested sites (A, B), where leaf litter samples were taken, and the others.

It is immediately apparent from Table 1 that there is no correlation amongst site rankings for these 11 taxa based on these data. Each row of the table places the five sites in a different rank order. If the numbers of identifiable species per site can be taken as estimates of species richness it is clear that the answer to the question "Which site is most diverse?" depends entirely upon which taxa are chosen to represent diversity.

There are few points of agreement within Table 2 except that both Amphipoda and Coleoptera give site ranking ABCDE, both Acari and Diptera give CBADE, and both Chilopoda and Diplopoda repeat the CBA — signal. Each other taxon gives a different site ranking. Of the taxa identified to species level (and listed in Table 1), only Coleoptera gives the same site ranking (ABCDE) on both the species-number and ordinal-abundance measure.

Table 3 demonstrates that site rankings vary according to taxonomic expertise, with RTUs (Trueman and Cranston, this volume), sometimes providing different site rankings to

Table 1. Numbers of identified* species by site; abundance and ranking of sites for each group. (Pooled observations: three sampling periods and all trapping methods)

Taxon	Site					Total	Rank
	A	B	C	D	E		
Diplopoda	7	5	4	0	0	10	ABC —
Chilopoda	3	7	3	0	0	9	BAC —
Araneae (Feb. + May)	19	28	17	7	6	54	BACDE
Collembola (Feb. only)	46	34	25	16	19	78	ABCED
Thysanoptera	2	11	6	4	4	17	BCDEA
Odonata	1	1	6	2	9	14	ECDAB
Coleoptera (Feb. + May)	63	46	18	13	10	132	ABCDE
Diptera?	13	18	25	18	20	32	CEBDA
Chironomidae: Feb only	18	12	5	-	7	35	ABEC -
Formicidae	7	15	21	11	9	36	CBDEA
Other Hymenoptera	42	47	10	7	10	113	BACED
TOTALS: all taxa	221	225	140	78	94	530	BACED

*NB: The category "identified" does not equate to "Fully Named". Up to one-half the specimens in most taxa could be identified only to a species number, a voucher collection number or some similar code.

? Terrestrial taxa, family level

Table 2. Numbers of specimens by site and "order". Large pitfall traps, combined totals for February, May and August

	Site					Rank
	A	B	C	D	E	
Amphipoda	194	149	44	13	11	ABCDE
Acari	233	248	290	156	101	CBADE
Araneae	63	107	88	28	13	BCADE
Opilionida	16	11	97	4	1	CABDE
Chilopoda	1	2	14	-	-	CBA —
Diplopoda	7	11	20	-	-	CBA —
Collembola	563	694	414	238	375	BACED
Orthoptera	7	5	771	9	-	CDAB -
Hemiptera	43	7	38	11	12	ACEDB
Thysanoptera	1	-	16	2	13	CEDA -
Coleoptera	106	103	61	22	19	ABCDE
Diptera	137	152	194	84	63	CBADE
Lepidoptera	4	6	6	5	14	CDBA -
Formicidae	20	37	370	162	22	CDBEA
Other Hymenoptera	15	42	42	9	4	BCADE

Table 3. Site rank orders for species numbers against RTU for representative taxa and samples.

		A	B	C	Site D	E	Rank
Araneae (Feb)	RTU	30	10	12	6	4	ACBDE
	Spp.	14	24	11	5	4	BACDE
Araneae (May)	RTU	10	15	1	9	5	BACDE
	Spp.	16	21	16	5	4	BACDE
Chilopoda (all)	RTU	2	4	3	-	-	BCA —
	Spp.	3	7	3	-	-	BCA —
Diplopoda (all)	RTU	11	5	7	-	-	ACB —
	Spp.	7	5	4	-	-	ABC —
Collembola (Feb)	RTU	23	16	11	10	11	ABCED
	Spp.	51	31	24	15	18	ABCED
Thysanura (Feb)	RTU	-	6	5	3	6	BECD -
	Spp.	-	7	3	3	4	BECD -
Thysanura (May)	RTU	-	12	3	1	1	BCDE -
	Spp.	-	7	4	1	1	BCDE -
Formicidae (Feb)	RTU	8	12	16	9	7	CBDAE
	Spp.	5	12	17	11	6	CBDEA
Coleoptera (May)	RTU	37	17	9	5	3	ABCDE
	Spp.	36	17	9	5	3	ABCDE

taxonomist's species (e.g., spiders, Collembola). Furthermore, site rankings change with season (e.g., spiders in February and May).

Plants

The lists of plant species can be summarised as follows:

Site A: Four tree species present (*Eucalyptus regnans*, *Nothofagus cunninghamii*, *Atherosperma moschatum*, *Acacia dealbata*), and eight understorey vascular plants. Several mosses, lichens and fungi (i.e., a relatively large non-vascular component). Total: 12 species of vascular plants within the area from which the invertebrate samples were taken.

Site B: One species of large tree (*Eucalyptus sieberi*), nine identified understorey and ground plants and a number of other small vascular plants lacking fruiting bodies, etc, and so not fully identifiable to species level at this time of year. Total: 10 identified (to species) and approximately 15 species of vascular plants within the sampling area.

Site C: One tree species (*Eucalyptus amygdalina*) plus 35 shrub and ground-cover species, plus six other shrubs and ground covers. Total: at least 42 species of vascular plants within the sampling area.

Site D: One tree species (*Eucalyptus amygdalina*) located just outside the sampling area, plus six shrubs and 23 other plants identifiable to

species level and several other not fully unidentifiable sedges, pea-flowering genera and orchids. Total: at least 35 species of vascular plants within the sampling area.

Site E: One dominant plant (buttongrass: *Gymnoschoenus sphaerocephalus*), four identifiable trees or shrubs plus some unidentified sedges. Total: 6–8 species of vascular plants within the sampling area.

We took the absolute number of vascular plant species at sites A–E as being 12, 15, 42, 35 and 7 species, respectively, giving site rank order CDBAE.

Discussion

Specific hypotheses

We set out to test two specific hypotheses, namely:

1. there exist predictor set(s), defined as one or more groups of taxa the diversity of which predicts the diversity of other taxa;
2. there is a relationship between arthropod diversity and the diversity of conventionally surveyed taxa.

Table 1 demonstrates the virtually complete lack of correlation in rank order of sites as measured by the numbers of species (or, for Dip-tera, families) in different orders or other higher categories. Table 2 shows the lack of correlation in rank order of sites measured by the numbers

of specimens observed by pitfall trapping. Table 3 showed, *inter alia*, that species site rankings and RTU site rankings each vary considerably across sampling occasions, at least for some taxonomic groups. We also noted seasonal differences in the patchiness (clumping) of some taxa, and patterns related to trapping method.

Exploratory statistical analyses, conducted to investigate these hypotheses in greater depth, confirm and further quantify these general findings. That is:

1. although the possibility of biodiversity predictors cannot be denied, as yet we have failed to discover any taxon or subset of taxa which could be used to predict the diversity of other taxa across our sample of five sites;

2. there is no close correlation between arthropod diversity and diversity as measured by a count of the vascular plant species at each of our sites (at least for the majority of arthropod taxa).

Predictor sets

In relation to the search for indicators, New (1993) has suggested an "ecological" approach to defining which subsets of taxa are most suitable in biodiversity assessment and monitoring. The best suite would give "sound and subtle ecological information: concentrating on the groups of invertebrates sensitive to environmental change and whose incidence and abundance can thereby be used to assess and ensure the well-being of Earth's major ecosystems" (New, 1993: 626). Further important qualities for the selected taxa would include having a well-established taxonomy, being geographically widespread and abundant, being habitat-specific and being amenable to sampling. Other authors (e.g., Kremen et al., 1993; Pearson, 1994; Stork, 1994) have offered similar lists of desirable and/or required attributes, usually adding "ecological" or "trophic" diversity to the attributes listed in New (1993). To date, no author has suggested a specific "basket" of taxa which would have the attributes being sought.

Others have taken a single-taxon approach, giving reasons why their own specialist group is a good indicator, either of diversity or else environmental change. The most commonly studied taxa worldwide include butterflies, selected beetle families, spiders, bees and ants. In Australia, the use of ants as an indicator of terrestrial invertebrate diversity has been suggested (Greenslade, 1985; Andersen, 1987, 1990), as has use of Collembola (e.g., Greenslade, 1993). Ubiquity, ease of sampling, high

intra-group diversity and high ecological importance have been among the arguments used to justify these choices. However, although the diversity in each taxon shows undoubted relationships with ecological variables that may themselves be important in land management decisions, in no case is the capacity to predict meaningful components of the diversity of other taxa more than an untested assertion.

None of the authors cited above has distinguished between environmental indication and biodiversity prediction, as alluded to in our introduction. None-the-less it is instructive to examine the performance of the commended groups as predictors. The results presented in Tables 1–3 indicate that, for our five study sites, neither ant nor collembolan species richness predicts anything. Further, the discrepancies amongst site rankings for different taxa are such that no taxon or subset of taxa from amongst those which we were able to evaluate gives site rankings which predict the rankings obtained from other taxa. There is no evidence here for taxa which could be used as a predictor set.

Congruence with conventional estimators

Comparing site rank order for plants and invertebrate animals, there is little congruence. A test of statistical significance for rank order correlation among sites is available (e.g., Southwood, 1978: 280–282), but owing to the small sample size (five sites) requires complete agreement in rank order, without ties, to achieve the 95% confidence level. The site rank order for plant species (CDBAE) exactly matches that for ants (Formicidae), as shown in Table 1. We can conclude that ant species diversity and plant species diversity are well correlated. The ordinal signal for ants in large pitfall traps (site rank order based on numbers of specimens rather than species: Table 2; CDBEA) almost matches this pattern, and the RTU estimate from the February samples (all trapping methods, RTU count: Table 3; CBDAE) again is close, disagreeing only in the relative positions of sites B and D although the corresponding count of actual species (Table 3: CBDEA) differs at both DB and AE. Thus, sampling by more than one trapping method and across more than one sampling period may be necessary in order to recover the plant species diversity signal using ants as a surrogate.

Conclusions

It is imperative that for Australia's considerable biological diversity to be properly assessed,

managed and conserved, the major components of that biodiversity must be measured in relevant ways and within an acceptably short time frame. Current biodiversity assessment practice, in Australia as elsewhere, has focussed on vertebrates and flowering plants to the virtual exclusion of the more abundant, diverse, and in many cases ecologically more important invertebrate animals. A grossly insufficient "species richness" signal is obtained from the vertebrates and angiosperms alone.

Concentration on a narrow set of large and charismatic organisms stems from a perceived lack of knowledge of, and appropriate methods for assessing, the contribution of invertebrate richness to biodiversity value, although this is refuted by Coddington et al., (1991), Longino (1994) and Hammond (1994), amongst others. An additional misconception is the belief that actions designed to protect charismatic taxa will also protect invertebrates.

It is an attractive concept that there may exist certain taxonomic groups that can act as predictors of biodiversity in general. Indeed, we might expect such taxa if the historical factors that lead to differential and concerted patterns of survival and extinction between areas, operating across a range of unrelated taxa, lead to congruent patterns of species richness across taxonomic groups. Thus, high speciosity might be expected in areas (sites) where sustained benevolent conditions have promoted long-term survival and allowed complex mutualistic associations to develop (areas that may be termed refugia). Relatively low species richness across many taxa might be expected where adverse or fluctuating conditions have promoted community instability, causing high rates of species turnover and extinction and providing reduced opportunities for the development of coevolutionary complexity. The fact that we were unable to identify any predictor sets is no guarantee that such sets cannot be found. Undoubtedly, some patterns of correlation exist and they may well be useful in biodiversity assessment, at least in some biological systems, and further study is warranted.

We concur with recent advocacy of practical approaches to species richness assay (e.g., Hammond, 1994; Longino, 1994; Colwell and Coddington, 1995), but are not of the view that species richness, *per se*, is sufficient indicator of conservation value. Since assessment of invertebrate species richness remains fraught with difficulties caused by seasonality, cryptic behaviour, and stochasticity in invertebrate assemblages, measures of the class we have been

investigating may never, of themselves, give sufficient information on which conservation decisions can be based.

Why should a modern "snapshot" of a constantly shifting equilibrium between processes of continuity and change, species formation and extinction, be expected to provide a firm basis for the allocation of conservation resources? Is a species-poor community from an extreme environment (or, for example, from an island with naturally limited diversity) worthy of less conservation effort than is a highly diverse community? Inevitably, decisions on relative values of richness will be partially subjective, leading to development of more objective ideas, such as those concerning complementarity and phylogenetic measures of taxonomic diversity (e.g., Vane-Wright et al., 1991; Faith, 1992; Crozier, 1992; Margules, 1992).

Assessments of biological diversity need not necessarily be based solely on new survey data. A considerable physical database, including invertebrate taxa, exists in the form of museum and herbarium collections, and significant information on distributions, etc. is available in electronic form. Modelling tools (such as BIOCLIM, Busby, 1990) can be used to make site or area diversity predictions from such data, and at least for some taxonomic groups may substitute partially for new survey work. The current disadvantages of scattered repositories and shortage of electronically-stored data are being addressed for many taxa, although invertebrates lag behind vertebrates and angiosperms in coverage. A rapid field survey by way of testing (ground-truthing) the predictions of the models will, of course, still be necessary in all cases, first to correct for any mis-prediction and second to allow for anthropogenic or other changes in local conditions since the time at which data on which the prediction is based were collected.

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References

- Abbott, I., 1974. Numbers of plant, insect and land bird species on nineteen remote islands in the Southern Hemisphere. *Biological Journal of the Linnean Society* 6: 143–152.
- Andersen, A.N., 1987. Ant community organisation and environmental assessment. Pp. 43–52 in: Majer, J.D. (ed.). *The role of invertebrates in conservation and biological survey*. Western Australian Department of Conservation and Land Management: Perth.
- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–357.
- Austin, M.P. and Heyligers, P.C., 1989. Vegetation survey design for conservation: gradsect sampling of forests in north-eastern New South Wales. *Biological Conservation* 50: 13–32.
- Beattie, A.J. and Oliver, I., 1994. Taxonomic Minimalism. *Trends in Ecology and Evolution* 9: 488–490.
- Beattie, A.J., Majer, J.D. and Oliver, I., 1993. Rapid biodiversity assessment: a review. Pp. 4–14 in: Beattie, A.J., Majer, J.D. and Oliver, I. (eds). *Rapid biodiversity assessment: Proceedings of the Biodiversity Assessment Workshop, Macquarie University 1993*. Research Unit for Biodiversity and Bioresources, School of Biological Sciences, Macquarie University: Sydney.
- Beccaloni, G.W. and Gaston, K.J., 1994. Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation* 71: 77–86.
- Brower, A.V.Z., 1995. Taxonomic minimalism. *Trends in Ecology and Evolution* 10: 203.
- Busby, J.R., 1990. BIOCLIM — A bioclimate analysis and prediction system. Pp. 64–68 in: Margules, C.R. and Austin, M. P. (Eds). *Nature conservation: cost effective biological surveys and data analysis*. CSIRO: Melbourne.
- Campbell, I.C., 1995. Taxonomic minimalism. *Trends in Ecology and Evolution* 10: 203.
- Coddington, J.A., Griswold, C.E., Silva Dávila, D., Peñaranda, E. and Larcher, S.F., 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pp. 44–60 in: Dudley, E.C. (ed.). *The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*. Dioscorides Press: Portland.
- Colwell, R.K. and Coddington, J.A. 1995. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345: 101–18.
- Cranston, P.S., 1993. Rapid biodiversity assessment in aquatic ecosystems. Pp. 15–20 in: Beattie, A.J., Majer, J.D. and Oliver, I. (eds), *Rapid biodiversity assessment: Proceedings of the Biodiversity Assessment Workshop, Macquarie University 1993*. Research Unit for Biodiversity and Bioresources, School of Biological Sciences, Macquarie University: Sydney.
- Cranston, P.S., and T. Hillman., 1992. Rapid assessment of biodiversity using "biological diversity technicians". *Australian Biologist* 5: 144–154.
- Crozier, R.H., 1992. Genetic diversity and the agony of choice. *Biological Conservation* 61: 11–15.
- DEST (Federal Department of the Environment, Sport and Territories), 1995. *National strategy for the conservation of Australia's biological diversity. Draft*. DEST: Canberra.
- Disney, R.H.L., 1986. Assessments using invertebrates: posing the problem. Pp. 271–293 in: Usher, M.B. (ed.), *Wildlife conservation evaluation*. Chapman and Hall: London.
- Faith, D.P., 1992. Systematics and conservation: on predicting the feature diversity of subsets of taxa. *Cladistics* 8: 361–373.
- Greenslade, P., 1993. Australian native steppe-type landscapes: neglected areas for invertebrate conservation in Australia. Pp. 51–73 in: Gaston, K.J., New, T.R. and Samways, M.J. (eds), *Perspectives on insect conservation*. Intercept Press: Andover, UK.
- Greenslade, P.J.M., 1985. Some effects of season and geographical aspect on ants (Hymenoptera: Formicidae) in the Mt Lofty Ranges, South Australia. *Transactions of the Royal Society of South Australia* 109: 17–23.
- Hammond, P.M., 1994. Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London B* 345: 119–136.

- Holloway, J.D. and Stork, N.E., 1991. The dimensions of biodiversity: the use of invertebrates as indicators of human impact. Pp. 37–61 in: Hawksworth, D.L. (ed.), *The biodiversity of microorganisms and invertebrates: its role in sustainable agriculture*. CAB International: UK.
- Johnson, R.K., 1995. The indicator concept in freshwater biomonitoring. Pp. 11–27 in: Cranston, P.S. (ed.), *Chironomids: from genes to ecosystems*. CSIRO Publications: Melbourne.
- Kitching, R.L., 1993. Towards biodiversity assessment — lessons following studies of arthropods of rainforest canopies. Pp. 26–30 in: Beattie, A.J., Majer, J.D. and Oliver, I. (eds), *Rapid biodiversity assessment: Proceedings of the Biodiversity Assessment Workshop, Macquarie University 1993*. Research Unit for Biodiversity and Bioresources, School of Biological Sciences, Macquarie University: Sydney.
- Kremen, C., 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2(2): 202–217.
- Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. and Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7: 796–808.
- Landres, P.B., Verner, J. and Thomas, J.W., 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2: 316–328.
- Longino, J.T., 1994. How to measure arthropod diversity in a tropical rainforest. *Biology International* 28: 3–13.
- Margules, C.R., 1985. *The Wog Wog habitat patch experiment: background, objectives, experimental design and sample strategy*. Technical Memorandum 85/18. CSIRO Institute of Biological Resources: Canberra.
- New, T.R., 1993. Angels on a pin: dimensions of the crisis in invertebrate conservation. *American Zoologist* 33: 623–630.
- Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4: 355–364.
- Oliver, I., 1993. Rapid biodiversity assessment and its application to fauna conservation in production forests. Pp. 31–34 in: Beattie, A.J., Majer, J.D. and Oliver, I. (eds), *Rapid biodiversity assessment: Proceedings of the Biodiversity Assessment Workshop, Macquarie University 1993*. Research Unit for Biodiversity and Bioresources, School of Biological Sciences, Macquarie University: Sydney.
- Oliver, I. and Beattie, A.J., 1994. A possible method for the rapid assessment of biodiversity. Pp. 133–136 in: Forey, P.L., Humphries, C.J. and Vane-Wright, R.I. (eds), *Systematics and conservation evaluation*. Clarendon Press: Oxford.
- Pearson, D.L., 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society of London, B* 345: 75–79.
- Pearson, D.L. and Cassola, F., 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicinellidae): indicator taxon for biodiversity and conservation. *Conservation Biology* 6: 376–91.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. and Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365: 335–337.
- Southwood, T.R.E., 1978. *Ecological methods with particular reference to the study of insect populations*. 2nd. edn. Chapman and Hall: London.
- Stork, N.E., 1994. Inventories of biodiversity: more than a question of numbers. Pp. 81–100 in: Forey, P. L., Humphries, C. J. and Vane-Wright R. I. (eds), *Systematics and conservation evaluation*. Systematics Association Special Volume No. 50. Clarendon Press: Oxford.
- Thackway, R. and Cresswell, I.D., 1992. *Environmental regions of Australia. a user oriented approach*. Environmental Resources Information Network (ERIN): Canberra.
- Trueman, J.W.H. and Cranston, P.S. 1994. *An evaluation of some methods of rapid biodiversity assessment for estimating arthropod diversity*. Report to the Department of the Environment, Sport and Territories. 66 pp. Unpublished.
- Vane-Wright, R.I., Humphries, C.J. and Williams, P.H., 1991. What to protect? — systematics and the agony of choice. *Biological Conservation* 55: 235–254.
- Weaver, J.C. 1995. Indicator species and scale of observation. *Conservation Biology* 9: 939–942.
- Williams, P.H. and Gaston, K.J., 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation* 67: 211–217.
- Wilson, E.O., 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1: 344–346.
- Yen, A.L., 1987. A preliminary assessment of the correlation between plant, vertebrate and Coleoptera communities in the Victorian mallee. Pp. 73–88 in: Majer, J. D. (ed.), *The role of invertebrates in conservation and biological survey*. Western Australian Department of Conservation and Land Management (CALM): Perth.

BIODIVERSITY AND BIOGEOGRAPHIC RELATIONSHIPS OF SELECTED INVERTEBRATES FROM URBAN BUSHLAND REMNANTS, PERTH, WESTERN AUSTRALIA

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Abstract

Harvey, M.S., Waldock, J.M., How, R.A., Dell, J. and Kostas, E., 1997. Biodiversity and biogeographic relationships of selected invertebrates from urban bushland remnants, Perth, Western Australia. *Memoirs of the Museum of Victoria* 56(2): 275-280.

The results of a continuous pitfall trapping programme designed to collect ground-dwelling invertebrates on the Swan Coastal Plain, Perth, is documented. Of the groups identified to date (Arachnida, except Acarina and some Araneae, scolopendrid and scutigrid centipedes, cockroaches and baeine wasps), 181 species have been identified, indicating a rich assemblage. Average linkage clustering analysis (UPGMA) of similarity indices derived from species abundance data is presented for some groups, which show differing patterns in relation to vegetation and landform. Larger bushland remnants have higher species richness and abundance.

Introduction

The depletion of native vegetation during urbanisation in many regions of the world has had an obvious and deleterious effect on much of the original biota, raising concerns for the long-term welfare of not only individual species, but of entire ecological communities. The rapid growth of Australian cities since European settlement has led to large-scale clearance and degradation of substantial areas of pristine bushland such that concerns have been expressed over the long-term viability of constituent species.

Perth is the largest city in Western Australia and is mostly situated on the Swan Coastal Plain centred on a latitude of approximately 32°S. It experiences a predominately Mediterranean climate consisting of hot, dry summers and wet winters where more than half of the annual rainfall of 837 mm falls between June and August. The coastal heaths and woodlands of the Swan Coastal Plain and surrounding regions are recognised internationally for their high diversity of both plants (Marchant, et al., 1987) and reptiles (How and Dell, 1994). However, the taxonomic and biogeographic relationships of the invertebrate fauna of this area is generally poorly documented.

A survey was commenced in 1993 to describe and interpret the ground fauna, both invertebrate and vertebrate, of remnant urban bush-

land patches on the Swan Coastal Plain, a region characterised by a series of landforms of Pleistocene age and a diverse array of floristically rich vegetation types. We here present preliminary data on a selection of invertebrates, including predacious (arachnids and centipedes), detritivorous (cockroaches) and parasitic (baeine wasps) groups, and examine the distribution of some species, their probable origins, and the biogeographic significance of these groups on the Swan Coastal Plain. This work is seen as a necessary precursor to any investigation into the effect that urbanisation might have on the remaining biota.

Methods

During the present study, which is the first of a 3-year program designed to investigate 12 or more locations on the Swan Coastal Plain, a total of 15 sampling sites were selected from four locations. These were selected so that a broad array of soil type and vegetation communities were sampled representing locations on four major landforms, including the more recent dune systems of Bold Park in the west, to the sands and colluvial clays and gravels of Talbot Road Reserve in the east.

Two of the four sites in Bold Park (BP) are on the Spearwood Dune System. Site BP3 is a *Banksia attenuata*/*B. menziesii* low woodland over low heathland on a dune top. Site BP4 is a Tuart

Eucalyptus gomphocephala woodland in an interdunal swale. Sites BP1 and BP5 are low heathlands on the coastal Quindalup Dune System.

All three sites at Tuart Hill (TH1–3) are Jarrah *Eucalyptus marginata* open woodland with a *Banksia attenuata* and *B. menziesii* low woodland understorey over diverse heathland on pale brown sands of the Spearwood Dune System.

Three of the four Perth Airport sites (PA) are on quartz sands of the Bassendean Dune System. PA5 is a dense low heathland, PA7 is a winter-inundated *Melaleuca preissiana* woodland, PA8 is a low woodland of *Banksia attenuata* and *B. menziesii* over low heathland. PA6 is a mixed shrubland apron of the Spearwood Sand System over Bassendean Sands.

Of the four Talbot Road sites (TR), sites TR1 and TR4 are on quartz sands of the Bassendean Dune System. TR1 is an open woodland of Jarrah *Eucalyptus marginata* with an understorey of *Banksia menziesii* and low heathland. TR4 is a *B. menziesii* low woodland over a low heathland. TR2 is a Marri *E. calophylla* woodland over low heathland on laterite/clay soils. TR3 is a *E. calophylla* woodland over *Hakea lissocarpa* shrubland on quartz sands similar to TR1 and TR4.

The invertebrate fauna was sampled solely by the use of pitfall traps placed flush with the ground at each of the sites. Ten 2 litre plastic ice-cream containers set with approximately 400 ml of ethylene glycol were placed 5–10 m apart. They were covered with linoleum floor tiles set approximately 10 cm above the top of the container to exclude rain and leaves. The traps were cleared every 6 weeks for a 12 month period, and the samples stored in 75% ethyl alcohol until they were sorted in the laboratory.

Several target groups were selected for detailed identification (ordinal names follow Harvey and Yen, 1989), which included arachnids belonging to four orders (Araneae, Scorpionida, Pseudoscorpionida, Opiliones), centipedes belonging to two orders (Scolopendrida and Scutigera), cockroaches (Blattodea) and the parasitic wasps of the tribe Baeni (Scelionidae). Several arachnid and centipede groups were excluded from the analysis due to uncertainties with species level identifications: these included all of the Acarina and several families of Araneae, such as the Gnaphosidae (Arachnida), and the Geophilida and Lithobiida (Chilopoda). The data matrix is presented in more detail in How et al. (1996).

Similarity between sites was calculated using

the Renkonen Index from the Biodiv (1993) package.

$$I = \sum_i \min(P_{ij}, P_{ik})$$

where P_{ij} is the proportion of the i th species in the j th sample and P_{ik} is the proportion of the i th species in the k th sample. The derived matrix was clustered using the UPGMA method.

Results and discussion

A total of 181 species was collected and identified, comprising 103 spiders, 3 harvestmen, 4 pseudoscorpions, 3 scorpions, 6 scolopendrid centipedes, 1 scutigera centipede, 34 cockroaches and 27 baenine wasps.

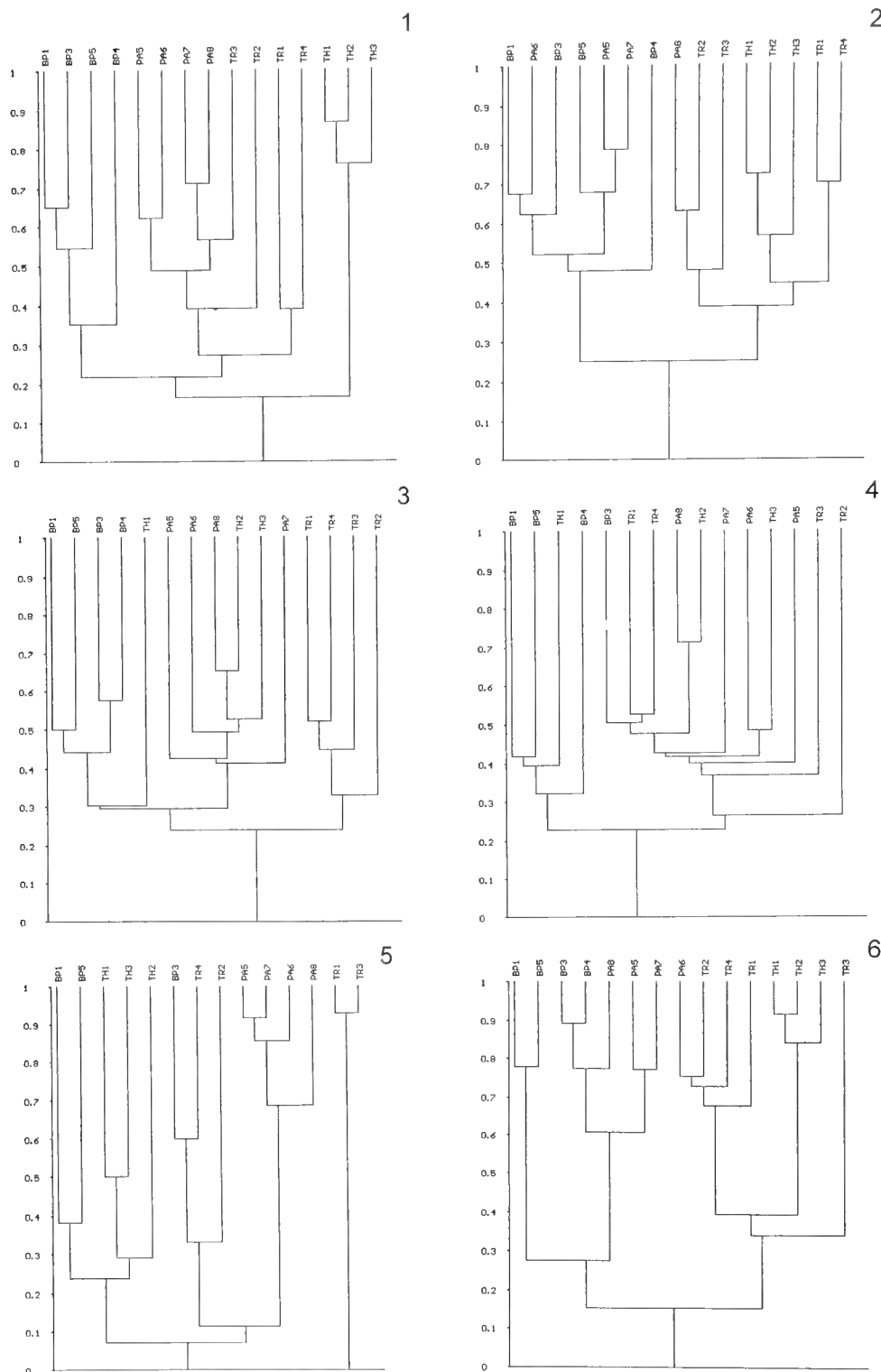
A total of 66 species (36.5%) was collected from only a single location and, of these, 34 species (18.8%) were collected from only a single site, although some of these have been previously recorded from outside of the study areas and should not necessarily be used to indicate extreme endemism. For example, the pseudoscorpion *Geogarypus taylori* Harvey is widely distributed across much of southern Australia (Harvey, 1986), and yet was only collected at the four Bold Park sites during the present study. However, it has been taken from two other sites on the Quindalup dunes, Woodman Point and Mount Claremont, during later aspects of this study, and the species may be restricted to this dune system in the Swan Coastal Plain. The actinopodid spider *Missulena granulosa* Hogg was only represented by a single male from BP5, and yet is widespread in south-western Australia (based upon records in the Western Australian Museum). In addition, some predominately arboreal species were occasionally caught in the pitfall traps, and the apparent endemism of these species is probably due to a form of sampling bias. For example, of the five species of Heteropodidae collected, at least one (*Isopoda leishmanni* Hogg) is known to be extremely abundant throughout the Perth metropolitan region and elsewhere in southern Australia (Hirst, 1992).

Our preliminary documentation of invertebrate biodiversity shows considerable variation in the total number of species recorded from each site, ranging from 34 species at TR3 to 71 species at BP1 (Table 1).

The 181 species identified from 16 sites at the four locations sampled were subjected to similarity analyses of their composite assemblages. Similar data for the Baeni were also evaluated. These data are preliminary in that the project intends to document assemblages from over 30

Table 1. Total numbers of species of selected invertebrate groups from four locations on the Swan Coastal Plain, Perth.

Location Patch size (ha) Site	Bold Park 338				Perth Airport 400				Tuart Hill 9			Talbot Road 90				TOTAL
	BP1	BP3	BP4	BP5	PA5	PA6	PA7	PA8	TH1	TH2	TH3	TR1	TR2	TR3	TR4	
Araneae	36	31	26	30	30	32	28	19	30	15	27	20	30	17	15	103
Opiliones	1	1	1	1	3	3	3	3	2	2	2	1	0	0	1	3
Pseudoscorpionida	2	4	2	2	1	1	1	2	1	1	1	2	2	0	1	4
Scorpionida	2	1	1	1	1	2	0	2	3	0	1	2	2	2	2	3
Scolopendrida	4	2	2	2	4	4	3	5	2	2	3	3	5	2	3	7
Scutigerida	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Blattodea	14	17	16	12	16	18	8	8	8	10	6	11	13	9	11	34
Baeini	11	9	6	12	13	6	11	6	12	9	10	12	9	4	6	27
TOTAL	71	66	54	60	68	66	54	45	58	39	50	51	61	34	39	182



Figures 1–6. Dendrogram of similarity between sites for selected invertebrates using the Renkonen Index on abundance data and UPGMA clustering. Locations are identified by the following alpha codes: BP, Bold Park (sites 1, 3–5); PA, Perth Airport (sites 5–8); TH, Tuart Hill (sites 1–3); TR, Talbot Road (sites 1–4). 1, cockroaches; 2, baeline wasps; 3, arachnids and centipedes; 4, all spiders; 5, mygalomorph spiders; 6, centipedes.

sites at 11 locations throughout the Perth area.

Some interesting biogeographic patterns are evident in the data. In many analyses conducted, the three Tuart Hill sites have high similarity (e.g. Figs 1, 6), possibly due to their close vegetational and geographic similarity, but this may also be due to the low species counts obtained at each site (see Table 1).

Cockroaches (Fig. 1). The 34 species of cockroaches indicated three major clusters. TH is different to all other locations but high internal similarity is due to the low number of species, most of which are widespread across all landforms and vegetation types. The four BP sites also group together, with the three heath and shrubland sites (BP1, BP3, BP5) more similar to each other than to the woodland site BP4. TR1 and TR4 are heath and shrubland sandy sites on the Ridge Hill Shelf landform and have different assemblages to the remainder of the TR sites, and to the heaths and shrublands at PA on the Bassendean Dune System which show little similarity within themselves.

Baeine wasps (Fig. 2). Analysis of a group of parasitic wasps, the Baeini (Scelionidae), collected during the survey showed very little concordance with either vegetation or landform data. This can probably be explained by their biology which is more likely to track their spider hosts (Iqbal and Austin, 1997). Spiders as a group have low similarity between sites (Fig. 4) and probably account for the Baeini pattern where neither geomorphic unit or vegetation type can account for the clustering (see below).

Arachnids and centipedes (Fig. 3). The examination of the entire arachnid and centipede assemblage documented thus far (120 species) indicates that there is low similarity between sites on either the same landform or those of similar vegetation type. Although BP and TR sites do form loose clusters, there is low similarity between them and with sites on the Bassendean Dune System (PA) or Spearwood Dune System (TH).

Spiders (Fig. 4). Being by far the most diverse (103 species identified thus far) and abundant arachnid group identified during the survey, the influence of the lack of assemblage pattern for either landform or vegetation type in this group will have influenced the cluster of Fig. 3 as well as Fig. 2. This lack of pattern can be explained by a number of factors, most importantly that spiders constitute a diverse assemblage with remarkably varying life history strategies and

ecological attributes (Humphreys, 1988; Churchill, 1997). The mobility of individuals may vary greatly between species, thus affecting their capture rate during the survey.

Much of the observed clustering in several analyses conducted can be attributed to either the low species count, or to the overriding influence of spiders (103 species) on the pattern depicted. Some of the arachnid and centipede groups surveyed were represented by very few species. These include the **mygalomorph spiders** (Fig. 5), of which only 13 species were collected, and 8 of these were found at only a single location. Indeed, site BP4 yielded no specimens during the survey. Of the remaining sites, TR1 and TR3 clustered strongly with each other and they possessed no similarity with the remaining sites. This is mostly due to the very low species counts at these sites: only a single species was collected at TR1 (*Teyl* sp.) and only 2 species at TR3 (*Teyl* sp. and *Aganippe* sp. 2), with *Teyl* sp. not being represented at any other site and *Aganippe* sp. only being found elsewhere at TR4. Similarly, all of the PA sites clustered strongly but much of this can be explained by the high percentage of several common species.

With only 7 species collected, the **scolopendrid and scutigrid centipedes** (Fig. 6) represent another low-species group. However, many species were collected in large numbers, indicating a stronger signal in the analysis. The two sites on the Quindalup Dune System, BP1 and BP5, showed strong similarity to each other, as did the three TH sites. Three of the four TR sites clustered strongly with PA6, but the very weak linkage of TR3 with other sites is difficult to explain.

The results presented here clearly indicate that four urban bushland remnants situated on the Swan Coastal Plain, possess very high spider and cockroach diversities, with moderate diversities for the other groups sampled. The influence of landform was evident, but not paramount, in several analyses, with the most obvious link being the strong similarity of the two sites situated on the Quindalup Dune System (BP1 and BP5).

An understanding of the biology of species comprising assemblages and their response to pitfall trapping is crucial to an interpretation of similarity dendrograms. The reptile assemblages of 17 locations in the Perth region show differing responses to landform or vegetation type depending on the family considered (How and Dell, 1994). Skink assemblages from sites on the same landforms are more similar than are those

from similar vegetation types on different landforms, while snakes and other lizards show little patterning with either criteria and are probably poorly sampled by pitfall trapping (How and Dell, 1994).

A range of factors have not yet been fully considered in relation to the invertebrate ground fauna of the remnant bushland patches. These include the size of the remnant, its recent fire history, and other perturbation factors, such as weed infestation, grazing and logging. We estimate that the range of many species will be substantially increased as this study continues, and we will use the additional data to test the preliminary associations between sites found in the present study.

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References

- Churchill, T.B., 1997. Spiders as indicator taxa: an overview. *Memoirs of the Museum of Victoria* 56: 331–337.
- Harvey, M.S., 1986. The Australian Geogarypidae, new status, with a review of the generic classification (Arachnida: Pseudoscorpionida). *Australian Journal of Zoology* 34: 753–778.
- Harvey, M.S. and Yen, A.L., 1989. *Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates*. Oxford University Press: Melbourne.
- Hirst, D.B., 1992. Revision of the genus *Isopeda* Koch (Heteropodidae: Araneae) in Australia. *Invertebrate Taxonomy* 6: 337–387.
- How, R.A. and Dell, J., 1994. The zoogeographic significance of urban bushland remnants to reptiles in the Perth region, Western Australia. *Pacific Conservation Biology* 1: 132–140.
- How, R.A., Harvey, M.S., Dell, J. and Waldock, J.M., 1996. Unpublished report submitted to Heritage Council of Western Australia.
- Humphreys, W.F. (1988). The ecology of spiders with special reference to the Australian fauna. In: Austin, A.D. and Heather, N.W. (eds), *Australian Arachnology*: 1–22. Australian Entomological Society: Brisbane.
- Iqbal, M. and Austin, A.D., 1997. Species richness and endemism of Baeine wasps (Hymenoptera: Scelionidae) in Australia. *Memoirs of the Museum of Victoria* 56: 455–459.
- Marchant, N.G., Wheeler, J.R., Rye, B.L., Bennett, E.M., Lander, N.S. and Macfarlane, T.D., 1987. *Flora of the Perth region*. Western Australian Herbarium: Perth.

PRELIMINARY OBSERVATIONS ON AWARENESS, MANAGEMENT AND IMPACT OF BIODIVERSITY IN AGRICULTURAL ECOSYSTEMS

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Abstract

Horne, P.A. and Edward, C.L., 1997. Preliminary observations on awareness, management and impact of biodiversity in agricultural ecosystems. *Memoirs of the Museum of Victoria* 56(2): 281–285.

Agricultural ecosystems are often considered to be biological 'deserts' because of the use of monocultures and pesticides. However, the species richness and abundance of invertebrates can be similar to that found in many natural ecosystems. This paper describes the diversity of surface-active carabid beetles and earwigs over 2 years in cropping land in the Wimmera region of Victoria and contrasts it with data from other ecosystems. Management practices such as tillage and stubble retention have an impact on some invertebrates, but extremely few studies have described effects on species considered beneficial. We present information on the relative number and likely impact of these beneficial species, particularly carabid beetles and earwigs. Information for farmers concerning invertebrates in agricultural ecosystems usually concentrates on pest species. An approach to raise awareness of invertebrate diversity is discussed.

Introduction

Agricultural ecosystems are generally less diverse than the natural ecosystems they replace because the aim of agriculture is to produce a limited number of species that we find useful (Altieri, 1994; Gerard, 1995). However, even within any given region and with a single crop type, there are many different management practices that can affect the composition of the invertebrate community. For example, use of pesticides (type, method and frequency of application), irrigation, tillage practices and rotations will often vary markedly between farms. Consequently, it is difficult to generalise about the effect of agriculture on diversity of invertebrates in even one region or crop type.

Overseas there has been research on using management practices such as encouraging populations of predatory (beneficial) insects such as carabid beetles and hoverflies on field margins (Sotherton, 1985; Asteraki, 1994; Dennis and Fry, 1992). Within fields, conservation tillage practices can change the relative abundance of some invertebrate species (Stinner and House, 1990). White snails (*Certhia virgata*), wireworms (Coleoptera: Elateridae) and false wireworms (Coleoptera: Tenebrionidae) are pests that are often favoured by conservation tillage and stubble retention. However, little is known in Australia of the effects of conservation tillage practices on most species, including pests.

Robertson et al. (1994) have described effects of tillage on a range of soil-dwelling organisms in Queensland and shown that zero tillage may enhance ecological sustainability of farms by essentially maintaining a good diversity of invertebrate species.

This paper describes the diversity of carabid beetles active on the soil surface of both conservation and conventional tilled field crops in the Wimmera (western Victoria). Numbers of carabid beetles are described and compared with results from other environments including grasslands.

The perception of invertebrates in agricultural ecosystems is often as pests, and so there are particular needs of farmers and other land managers to address regarding awareness of invertebrates and biodiversity (Horne et al., 1995). We describe the approach we have taken to increase awareness of insects other than pest species, and the value of these insects to farmers.

Materials and methods

The study site in the Wimmera was located on the Longerenong College of Agriculture and Horticulture campus (36°39'S; 142°16'E). Eight adjacent large (5 ha) blocks have been managed to demonstrate differences in cropping using different tillage practices (Williams, 1994). Our study concentrated in three of these blocks, Bl. 1 (Conventional tillage and fallow) Bl.6

(conservation tillage with stubble retention and no fallow) and Bl.7 (Conventional tillage and no fallow). Crops planted in these blocks from 1991 to 1995 were as follows: Block 1, wheat, chick peas, fallow, wheat, field peas; Block 6, faba beans, barley, chick peas, canola, faba beans; Block 7, chick peas, canola, faba beans, barley, chick peas. Crops are usually planted following autumn rains (often April) and harvested in summer (usually December or January).

Twenty pitfall traps, each consisting of a plastic container 11 cm diam. x 5 cm deep, half filled with ethylene-glycol, were placed in two parallel lines of 10 traps in each block. Traps were placed 50 m apart in the two lines, each line 25 m in from the long boundaries. Traps were run continuously from April 1993 until April 1995 and emptied weekly. Further details of methods are described by Horne and Edward (1995).

Macroinvertebrates greater than approximately 3 mm long were identified to species or morphospecies, with reference to the Museum of Victoria collection. To assist with improving farmers recognition of common invertebrates, small insect collections were made using an 8.5 x 11.5 cm clear plastic display case, containing 13 insect specimens. The insects were dried and glued to a base piece containing common names, and arranged in two groupings as "beneficial" or "pest" species. Notes with colour pictures of the insects and a short description of their biology

were prepared to accompany the collection. Farmers were asked (i) whether these kits had improved their knowledge of the diversity of insects in their crops and (ii) their opinion on whether these kits would be of useful to farmers in the Wimmera.

Results

Twenty-eight species of carabid beetles (Coleoptera: Carabidae) were recorded from the study site. The total number captured per year is indicated in Table 1. The most abundant species were *Rhytisternus* sp, *Mecyclothorax ambiguus* and *Simodontus brumneus*. Another abundant predatory species at this site was *Labidura truncata* (Dermaptera: Labiduridae), with more individuals found per year than any of the carabids.

The fact that there is no replication in this part of the study means that no firm conclusions about the relative abundance of invertebrates in conventional or conservation tilled crops can be made. However, it is evident that in both tillage systems there are many carabid and other insect species present (Tables 1 and 2), and data from a replicated trial (Horne and Edward, 1996) also indicate that some carabids are more abundant in conservation tilled crops. The year catch is commonly used in studies of carabid populations to indicate the relative abundance of

Table 1. Year catch of 15 species of the most abundant carabid beetles from 20 pitfall traps in each of the three blocks sampled.

Carabidae	Block 1 1993-94	Block 1 1994-95	Block 6 1993-94	Block 6 1994-95	Block 7 1993-94	Block 7 1994-95	Total
<i>Rhytisternus</i> sp.	376	169	371	219	353	112	1600
<i>Mecyclothorax ambiguus</i>	161	179	39	6	156	15	556
<i>Simodontus brumneus</i>	135	77	33	100	121	41	507
<i>Geoscaptus</i> sp.	53	11	43	54	67	17	245
<i>Clivina planiceps</i>	129	48	4	1	4	0	186
<i>Nemaglossa australis</i>	81	22	12	7	36	8	166
<i>Platia minima</i>	3	17	16	42	21	66	165
<i>Sarticus</i> sp. 1	15	8	20	7	10	11	71
<i>Harpalinae</i> spp.	5	9	4	1	30	6	55
<i>Promecoderus</i> sp.	2	3	6	7	10	4	32
<i>Chlaenius australis</i>	2	0	16	0	7	0	25
<i>Anomotarus</i> sp.	0	1	3	0	11	3	18
<i>Apotomus australis</i>	2	3	1	6	2	2	16
<i>Catadromus (lacordairei)</i>	1	1	2	1	3	2	10
<i>Clivina</i> nr. <i>dilutipes</i>	5	2	0	0	0	0	7
<i>Zuphium australe</i>	1	0	0	3	1	2	7

Table 2. Year catch of key species, 1993–94 and 1994–95.

Species	Block 1	Block 6	Block 7
<i>Rhytisternus</i> sp (Beneficial carabid)			
1993–94	376	371	353
1994–95	169	219	112
<i>Labidura truncata</i> (Beneficial earwig)			
1993–94	3,227	1,752	3,610
1994–95	800	1400	1244
<i>Pterohelaeus darlingensis</i> (Pest tenebrionid)			
1993–94	568	913	773
1994–95	825	1,014	1,380
<i>Gonocephalum adelaidea</i> (Pest tenebrionid)			
1993–4	475	295	441
1994–5	516	188	969

different species. The year catch over two consecutive years indicates that populations of carabid (and earwig) species, in Block 6 (conservation tillage) may be more stable than in the conventionally tilled blocks (Table 2). That is, although the numbers of *Rhytisternus* and *L. truncata* were not always higher in Block 6, their numbers remained similar between years. Numbers of these species in Blocks 1 and 7 changed markedly over the same period. The numbers of the carabids *Simodontus brumneus* and *Geoscaptus* captured from Block 6 also either increased from 1993–94 to 1994–95, or else decreased by a much smaller percentage than corresponding populations from Blocks 1 and 7 (Table 1).

Despite the abundance of carabid beetles, there was little or no awareness of their presence by the farmers with whom the results were discussed. Carabid beetles are just one group of invertebrates that are likely to have an impact on pest species. The poor awareness of these beetles was interpreted by us as indicative of the low level of awareness of invertebrate biodiversity in general. To address this problem we prepared and distributed to farmers small insect collections containing a few of the most abundant pest and beneficial species. Farmers' comments on the insect kits were favourable in that they believed they had improved their knowledge of what was of benefit in their crops and that not all insects were pests. They were seen as being particularly useful in identifying non-pest species and also prompted a greater interest in the invertebrate fauna of their crops.

Discussion

Agriculture is a major land-use in Victoria and other States in Australia. We believe that it is important that discussions on biodiversity do not only concern conservation areas or natural ecosystems, but should include agricultural ecosystems. It is generally accepted that agricultural activities such as ploughing reduce the biodiversity of fields but the biodiversity of agricultural ecosystems can be similar to other natural systems (Paoletti et al., 1992). If we consider just the Carabidae, some estimates of species richness from different environments are; 178 species in arable agricultural land in Ontario (Rivard, 1964, 1965), 127 species in South Dakota field crops (Kirk, 1971), 114 species in Italian forest (Pizzolotto and Brandmayr, 1990), 68 species in an urban Ruderal system in Germany (Gruttke and Weigmann, 1990), 59 species in English grasslands (Luff, 1990) and 22 species in Finnish taiga (Niemela, 1990). We found 28 species in the Wimmera, which is a significant native fauna (resident and transient) using these croplands. There is no estimate of the carabid fauna in nearby, undisturbed habitats with which to compare these figures.

Conservation-tilled areas have been found to increase invertebrate biodiversity when compared to conventionally-tilled areas (Stinner and House, 1990; Robertson et al., 1993). The stability of crop ecosystems is increased by reducing tillage and so conservation-tilled crops would be expected to provide habitat for more species than regularly disturbed land. The results of our

study are consistent with these findings, but also, we suggest that beneficial species are favoured by conservation tillage. At present farmers perceive a close link between conservation tillage and pests.

We suggest that there is reason to expect longer term benefits from conservation tillage in enhancing and maintaining stable populations of predatory species. Carabid beetles are well-known predators of a range of invertebrates and contribute to the biological control of insect pests in agricultural environments. If farmers' management practices result in increased numbers of carabid beetles then improved biological control of some pests should result. That is, based on the results of the Wimmera study, the improved management of the resident macro-invertebrate fauna will lead to better pest control for the farmer.

Many of the predatory species have an annual life-cycle and so it could also be expected that they could be relatively slow to respond to changes in pest (prey) populations. Farmers may quickly perceive a pest problem associated with conservation tillage but not notice a slower improvement in predatory species. It is important, if maintaining invertebrate biodiversity in agricultural ecosystems is an aim, to document the relative abundance of pest and beneficial species under different tillage regimes and to provide information on beneficial species to farmers. The approach of using insect kits and notes has been well received by farmers and advisors in our study. We recommend it to others looking to promote invertebrate biodiversity and conservation.

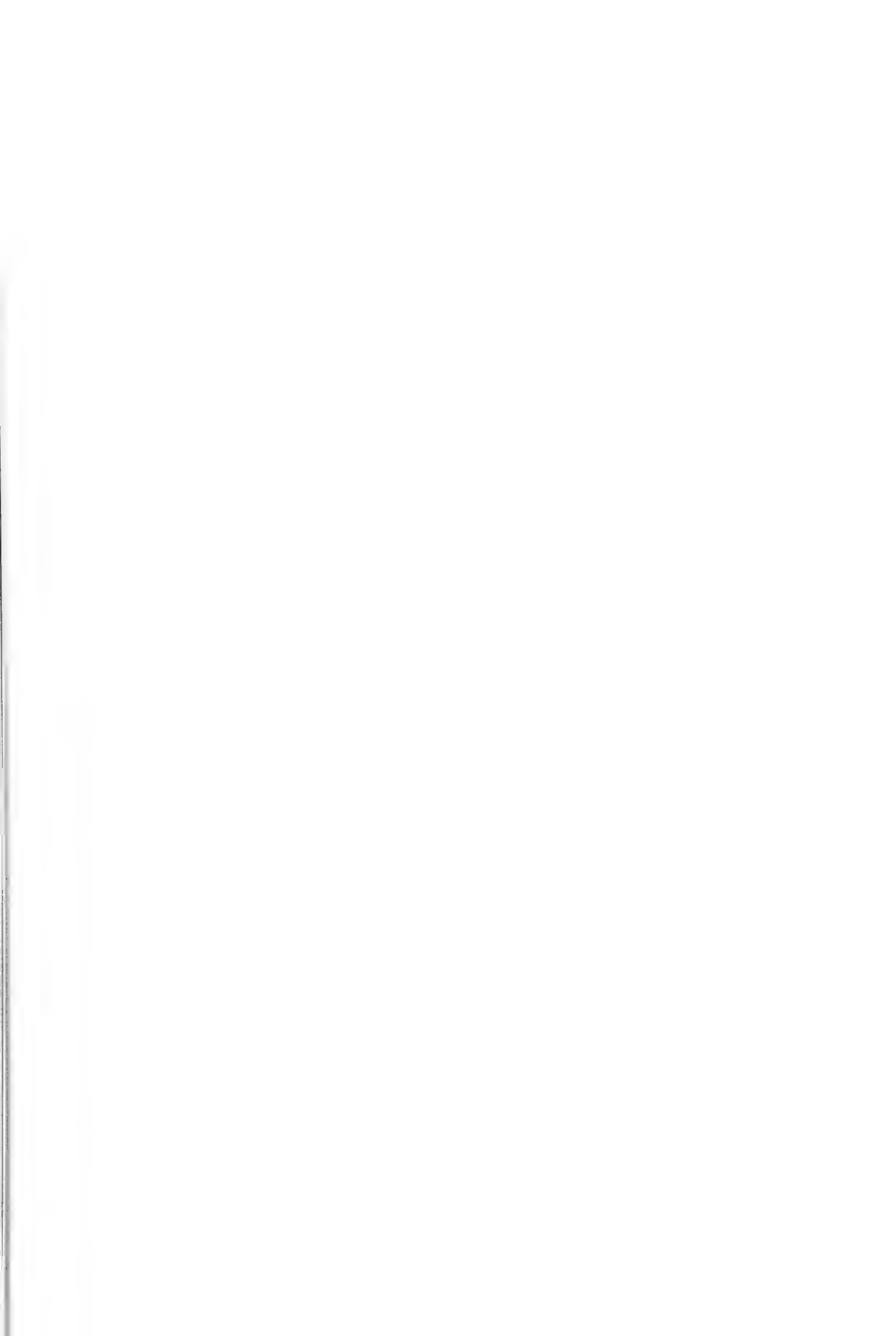
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References

- Altieri, M.A., 1994. *Biodiversity and pest management in agroecosystems*. Food Products Press: NY.
- Asteraki, E., 1994. The carabid fauna of sown conservation margins around arable fields. Pp. 229–233 in: Desender, K. et al. (eds), *Carabid beetles: ecology and evolution*. Kluwer.
- Dennis, P. and Fry, G.L.A., 1992. Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland. Pp. 95–115 in: Paoletti, M.G. and Pimentel, D. (eds), *Biotic diversity in agroecosystems*. Elsevier: Amsterdam.
- Gerard, P.W., 1995. Agricultural practices, farm policy, and the conservation of biological diversity. *Biological Science Report 4*, US Department of the Interior: Washington.
- Gruttke, H. and Weigmann, G., 1990. Ecological studies on the carabid (Coleoptera) fauna of a Ruderal ecosystem in Berlin. Pp. 181–189 in: Stork, N. (ed.), *The role of ground beetles in ecological and environmental studies*. Intercept: Andover.
- Horne, P.A. and Edward, C.L., 1995. Phenology and food preferences of *Labidura truncata* Kirby (Dermaptera: Labiduridae) in Western Victoria. *Journal of the Australian entomological Society* 34: 101–104.
- Horne, P.A. and Edward, C.L., 1996. Effects of tillage on invertebrates. Pp. 47–48 in: *Proceedings of the 11th Annual Seminar of the Wimmera Conservation Farming Association*. Longerenong College, March 1996.
- Horne, P.A., Short, M., Van Praagh, B.D. and Yen A.L., 1995. Invertebrate conservation and management on private land. Chapter 17, Pp. 135–141 in: Bennett, A., Backhouse, G. and Clark, T. (eds), *People and Nature Conservation*. Surrey Beatty and Sons.
- Kirk, V.M., 1971. Ground beetles in croplands in South Dakota. *Annals of the Entomological Society of America* 64: 238–241.
- Luff, M.L., 1990. Spatial and temporal stability of carabid communities in a grass/arable mosaic. Pp. 191–200 in: Stork, N. (ed.), *The role of ground beetles in ecological and environmental studies*. Intercept: Andover.
- Niemela, J., 1990. Spatial distribution of carabid beetles in the southern Finnish taiga: the question of scale. Pp. 143–155 in: Stork, N. (ed.), *The role of ground beetles in ecological and environmental studies*. Intercept: Andover.
- Paoletti, M.G., Pimentel, D. Stinner, B.R., 1992. Agroecosystem biodiversity: matching production and conservation biology. Pp. 3–23 in: Paoletti, M.G. and Pimentel, D. (eds), *Biotic diversity in agroecosystems*. Elsevier: Amsterdam.
- Pizzolotto, R. and Brandmayr, P., 1990. The carabid groupings of the Nebrodi Mountains in Sicily: ecological and historical indicators. Pp. 201–207 in: Stork, N. (ed.), *The role of ground beetles in ecological and environmental studies*. Intercept: Andover.
- Rivard, I., 1964. Carabid beetles (Coleoptera: Carabidae) from agricultural lands near Belleville, Ontario. *Canadian Entomologist* 96: 517–520.
- Rivard, I., 1965. Additions to the list of carabid beetles (Coleoptera: Carabidae) from agricultural lands near Belleville, Ontario. *Canadian Entomologist* 97: 332–333.
- Robertson, L.N., Kettle, B.A. and Simpson, G.B., 1994. The influence of tillage practices on soil

- macrofauna in a semi-arid agroecosystem in northeastern Australia. *Agriculture, Ecosystems and Environment*. 49: 149–156.
- Sotherton, N.W., 1985. The distribution and abundance of predatory Coleoptera overwintering in field boundaries. *Annals of Applied Biology* 1: 17–21
- Stinner, B.R. and House, G.J., 1990. Arthropods and other invertebrates in conservation-tillage agriculture. *Annual Review of Entomology* 35: 299–318.
- Williams, B., 1994. Management issues in a long-term farmer co-operative trial. Pp. 42–43 in: *Proceedings of Tillage Workshop*. Collaborative Centre for Land and Soil Research, Adelaide.



SOIL COLLEMBOLAN (INSECTA: COLLEMBOLA) ASSEMBLAGE STRUCTURE IN RELATION TO UNDERSTOREY PLANT SPECIES AND SOIL MOISTURE ON A EUCALYPT WOODLAND SITE

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Abstract

Rodgers, D., 1997. Soil collembolan (Insecta: Collembola) assemblage structure in relation to understorey plant species on a eucalypt woodland site. *Memoirs of the Museum of Victoria* 56(2): 287-293.

In order to investigate the hypothesis that the structure of soil collembolan assemblages beneath different plant species differs, four understorey plant species were studied in a eucalypt woodland site in southeast Queensland. Collembola were extracted from soil cores taken from ten replicate 1 m² sample plots for each of the four plant species: *Leptospermum attenuatum*, *Hibbertia stricta*, *Themeda triandra*, and *Xanthorrhoea johnsonii*. Relationships between the structure of the collembolan assemblage and the plant species were then examined using multivariate analysis of similarity (ANOSIM). The relationships between collembolan species abundance and plant species, and soil moisture contents were analysed using univariate methods.

Of the 25 species found, only one, *Willowsia* sp, differed significantly in abundance between plant species. *Willowsia* sp was significantly more abundant in association with *T. triandra* than with any other plant species ($\alpha = 0.05$). The abundance of many species was positively correlated with soil moisture. Soil texture did not vary significantly across the site but soil moisture did, such that *X. johnsonii* plots were found to be significantly drier than the other plot types, while *H. stricta* plots were significantly wetter than all others ($\alpha = 0.05$).

Analysis of similarity showed no relationship between the structure of the collembolan assemblages and the different plant species. Exploratory analyses of the relationship between soil moisture and assemblage dissimilarity showed high dissimilarity when two dry plots were compared and low when two wet plots were compared. This led to the hypothesis that dissimilarity would be higher in comparisons between *X. johnsonii* plots than in comparisons between *H. stricta* plots. This hypothesis was tested and accepted ($\alpha = 0.05$). It was concluded that more subtle distinctions in the structure of those collembolan assemblages associated with different plant species, might be found in a more experimentally oriented study in which soil moisture was controlled.

Introduction

The Collembola are known to respond to a number of environmental variables such as soil moisture and the food quality of the available microflora. Many plant species are known to have a distinctive effect upon these same variables. The potential therefore exists for some detectable association between the individual plant and collembolan species within a plant community.

Soil moisture is a critical factor in determining the distribution of Collembola. Low relative humidity generally results in increased migration and mortality and lower reproduction (Butcher et al., 1971). Although the Collembola lack a hard exoskeleton which might reduce rates of water loss (Fjellberg, 1985), a range of morphological adaptations such as waxed cuti-

cular tubercles (Greenslade, 1991), scales and setae may reduce transpiration from the body surface (Fjellberg, 1985). Transpiration rates may vary by an order of magnitude between species and there is evidence of a relationship between transpiration rate and habitat selection (Verhoef and Witteveen, 1980). Soil pH may also have an effect on the distribution and abundance of Collembola. Collembolan oviposition rates are known to be dependent on substrate pH (Butcher et al., 1971). With respect to dietary requirements, the Collembola can be considered to be primarily microphytophages and saprophytophages. Within this general description there is considerable evidence of dietary specialisation in the Collembola (e.g., Chapman et al., 1988; Klironomos et al., 1992; Shaw, 1985; Vegter, 1983; Wiggins and Curl, 1979), such that many species have been shown to feed pref-

entially on particular groups or species of fungi and algae. There is, therefore, a strong and clear relationship between the Collembola and many soil properties.

While variables such as soil moisture holding capacity, and pH may be considered intrinsic properties of different soils, there is substantial evidence that plants modify these soil characteristics. Because plant species may differ markedly with respect to water uptake and transpiration rates (Weier et al., 1982), and differences in plant architecture may have a distinctive effect on microclimate at the soil surface, different plant species may have differential effects on the soil moisture regime. Soil pH can be similarly affected. The absorption and secretion of different ionic species by plant roots may change the pH of the rhizosphere soil by as much as 2 pH units (Grubb and Suter, 1970; Foster, 1983; Bowen and Rovira, 1991). There is also substantial evidence of differential plant rhizosphere effects on the soil microflora. Curl and Trulove (1986), for example, found the ratios of microbial populations in rhizosphere soil to adjacent non-rhizosphere soil were 24, 6 and 3 for red clover, oats and barley respectively. Different plant species are also known to both inhibit and stimulate the growth of different microbial species via biochemically active root exudates (e.g. Bowen and Rovira, 1991; Curl and Trulove, 1986; Neill and Rice, 1971; Robinson, 1972; Mallik and Tesfai, 1988).

It is therefore clear that plants may substantially modify many of the soil properties that determine the distribution and abundance of the Collembola.

These plant-soil-collembolan interactions were hypothesised to play a role in the distribution of collembolan species in a eucalypt woodland site in Toohey Forest in southeast Queensland.

In this paper the relationship being examined is that between plant and collembolan species within a single plant community, rather than between plant communities (e.g., van der Drift, 1963; Hagvar, 1982; Knight and Read, 1969; Hutson and Veitch, 1983, 1987). It was also hypothesised that soil moisture was likely to vary across the site, and was almost certain to be an important factor in determining the nature of any variation in the structure of the collembolan assemblage.

To test these hypotheses a 1 Ha site was selected in Toohey Forest. The plant community on the site has been described by Coutts (1987) as, Planchon's stringybark (*Eucalyptus planchon-*

iana), broadleaved white mahogany (*Eucalyptus umbra* ssp. *carnea*) and smudgece (*Angophora woodsiana*) layered woodland to 20 m, and the soil is described by Stock (1987) as, a red-yellow podzolic of between 60 cm and 1 m depth. The understorey plant species *Hibbertia stricta*, *Lepidospermum attenuatum*, *Themeda triandra* and *Xanthorrhoea johnsonii* were selected for study. Beneath each plant species, ten plots of approximately 1 m² were randomly selected across the site, giving a total of 40 plots. Collembola were sampled from six randomly placed soil cores of 5 cm depth and 5 cm diameter from each plot. An additional soil sample of approximately 100g was taken from each plot for soil moisture and texture analyses. Extraction of Collembola from the soil cores was carried out by inverting undisturbed soil cores in a modified Tullgren funnel type system with a controlled temperature gradient of 20° across the sample (35° above, 15° below the sample), for 72 hours.

Standard univariate statistical methods were used in the data analysis. A variety of data transformations were used in an attempt to obtain homoscedasticity or to normalise percentage data, prior to the application of parametric testing procedures. Where transformed data remained heteroscedastic, nonparametric testing procedures were used. Multivariate analysis using analysis of similarity (ANOSIM) in the PRIMER statistical package (Plymouth Marine Laboratory, 1994) was carried out to test the significance of the ratio of within/ between group similarity of collembolan assemblages by plant species. The Bray/ Curtis association measure was calculated using the PATN statistical package (Belbin, 1995) to give an association data matrix for the analysis of similarity. The PATN statistical package was also used for Semi-strong-hybrid multidimensional scaling (MDS) to plot the similarity relationships of the samples in an ordination space. Experience with such analyses has shown that samples in which zero data are recorded for all species should be excluded from analysis since they are identical in terms of similarity, and tend to downweight any similarity between samples with nonzero data. Rare taxa also tend to add "noise" to such analyses and taxa with less than five nonzero data in a matrix were also excluded from multivariate analyses.

Results and discussion

A total of 3272 individuals and 25 species of Collembola were collected from the site, giving

an estimated density of 6943 Collembola/m² for the 0–50 mm soil horizon. The relative abundance of the species are plotted in Figure 1. A ranked species list is given in Table 1, which also shows the number of plots in which each species occurred. Variability in the abundance of all species was high as can be seen from the means and standard deviations in Table 1. Figure 1 reflects the fundamental structure of the collembolan assemblage of the site as a whole, and clearly shows the dominance of *Lepidocyrtus* sp. in terms of abundance, while Table 1 shows that *Lepidosira* sp. was the species found on most plots. The asymptotic form of the species/ area curve plotted in Figure 2 indicates that the majority of the soil collembolan species on the site were collected.

Willowsia sp. was the only species for which a significant difference was detected between plant species ($p = 0.05$). Post-hoc testing (Mann-Whitney U test) showed that *Willowsia*

sp. was significantly more abundant beneath *T. triandra* than any other plant species ($p = 0.05$). No significant differences were detected between plant species for any other collembolan species. Differences between plant species for the community descriptors, H' (Shannon-Weiner species diversity index), S (species richness) and N (number of Collembola per plot) were also nonsignificant. No Collembola were recorded in the sample from one of the *X. johnsonii* plots and this sample was therefore excluded from multivariate analyses. The seven least common species were found in less than five plots (see Table 1) and so these data were also excluded from the multivariate analyses.

The results of the analyses of similarity using species abundance and presence/ absence data (Table 2), show that there is no evidence of a significant structural distinction between collembolan assemblages associated with the different plant species.

Table 1. Collembolan species collected, ranked by abundance

Species	Total number collected	Mean number per plot	S.D.	Number of plots containing species
<i>Lepidocyrtus</i> sp.	1336	33.4	39.76	33
<i>Isotomiella prussiana</i> (Olivera & Deharveng, 1990)	500	12.5	15.94	31
<i>Lepidosira</i> sp.	452	11.3	16.78	37
<i>Dinaphorura</i> sp.	188	4.7	6.17	25
<i>Folsomides</i> sp.	152	3.8	6.23	24
<i>Mesogastrura</i> sp.	109	2.72	5.2	22
<i>Sinella</i> sp.	105	2.62	3.59	22
<i>Pseudosinella</i> sp.	92	2.3	4.27	20
<i>Megalothorax</i> sp.	92	2.3	4.37	15
<i>Isotoma</i> sp.	53	1.32	4.74	11
<i>Katianna</i> sp.1	44	1.1	2.43	15
<i>Lepidobrya</i> sp.1	33	0.83	1.57	13
<i>Sminthurus</i> sp.	30	0.75	1.15	16
<i>Willowsia</i> sp.	21	0.53	1.54	9
<i>Hemilobella</i> sp.	17	0.42	0.87	10
<i>Cephalochorutes</i> sp.	16	0.4	1.77	4
<i>Lepidocyrtoides</i> sp.	8	0.2	0.46	7
<i>Jeannenotia</i> sp.	8	0.2	0.46	7
<i>Homidia</i> sp.	5	0.13	0.52	3
<i>Katianna</i> sp.4	3	0.08	0.47	1
<i>Pseudoparonella</i> sp.	2	0.05	0.22	2
<i>Lepidobrya</i> sp.2	2	0.05	0.22	2
<i>Katiannini</i> gen. sp.	2	0.05	0.32	1
<i>Katianna</i> sp.3	1	0.03	0.16	1
<i>Katianna</i> sp.2	1	0.03	0.16	1

Table 2. Global and pairwise comparisons of assemblage similarity for collembolan abundance and presence/ absence data by plant species (ANOSIM).

Comparison	Within/between groups similarity	Significance level*	Within/between groups similarity	Significance level*
Global	0.039	13.5%	0.065	4.1%
<i>H. stricta</i> – <i>L. attenuatum</i>	0.02	52.8%	0.068	11.4%
<i>H. stricta</i> – <i>T. triandra</i>	0.005	36.5%	0.056	14.7%
<i>H. stricta</i> – <i>X. johnsonii</i>	0.078	10.4%	0.081	9.0%
<i>L. attenuatum</i> – <i>T. triandra</i>	0.044	19.4%	0.094	6.6%
<i>L. attenuatum</i> – <i>X. johnsonii</i>	0.047	20.0%	0.035	22.9%
<i>T. triandra</i> – <i>X. johnsonii</i>	0.072	11.9%	0.053	15.5%

*significance = % of 20000 random permutations which exceed actual within/ between groups similarity ratio. 5% significance threshold weighted for multiple comparisons = 0.36%.

Table 3. Texture analyses and moisture of soils beneath the four understorey plant species. (ANOVA: NS = non-significant p value; * = $p < 0.05$).

Understorey species	Soil texture		% Soil moisture content Mean \pm sd*
	% Sand ^{NS} Mean \pm sd	% Clay ^{NS} Mean \pm sd	
<i>X. johnsonii</i>	81.8% \pm 3.7	10.9% \pm 2.1	5.1% \pm 1.5
<i>L. attenuatum</i>	81.8% \pm 2.0	10.6% \pm 2.0	8.4% \pm 1.8
<i>T. triandra</i>	81.4% \pm 4.3	12.0% \pm 2.3	9.3% \pm 2.6
<i>H. stricta</i>	79.5% \pm 3.7	12.4% \pm 2.1	11.1% \pm 1.7

Table 4. Spearman Rank correlation for collembolan species abundance and community descriptors versus soil moisture. (* indicates significance at $\alpha = 0.05$).

Species	Rho
<i>Lepidocyrtus</i> sp.	0.592*
<i>I. prussianae</i>	0.346*
<i>Lepidosira</i> sp.	0.073 n.s.
<i>Dinaphorura</i> sp.	0.511*
<i>Folsomides</i> sp.	0.399*
<i>Mesogastrurasp.</i>	0.347*
<i>Sinella</i> sp.	0.458*
<i>Pseudosinella</i> sp.	-0.13 n.s.
<i>Megalothorax</i> sp.	0.366*
<i>Isotoma</i> sp.	0.089 n.s.
<i>Katianna</i> sp.1	0.484*
<i>Lepidobrya</i> sp.1	0.012 n.s.
<i>Sminthurus</i> sp.	0.241 n.s.
<i>Willowsia</i> sp.	0.019 n.s.
<i>Hemilobella</i> sp.	0.348*
Species richness — S	0.551*
Species diversity — H	0.451*
Total Collembola — N	0.500*

The primary hypothesis of this study must be rejected at this point. There is insufficient evidence to conclude that distinct collembolan assemblages are associated with the selected understorey plant species in this site. The apparent preference of *Willowsia* sp. for soils beneath *Themeda triandra* is worthy of further investigation. However *Willowsia* sp. made only a minor contribution to the structural character of the assemblage.

Table 3 shows that while there was no significant difference between plot types in soil texture, soil moisture was significantly different ($\alpha = 0.05$), with *H. stricta* plots being significantly wetter than other plot types and *X. johnsonii* plots being significantly drier than other plot types ($\alpha = 0.05$) (Fisher PLSD). As shown in Table 4, abundances of many of the collembolan species of the site were significantly and positively correlated with soil moisture content, as were the community descriptors S, H and N. Some variation in the structure of the collembolan assemblage on the site might therefore be expected to be associated with variation in soil moisture.

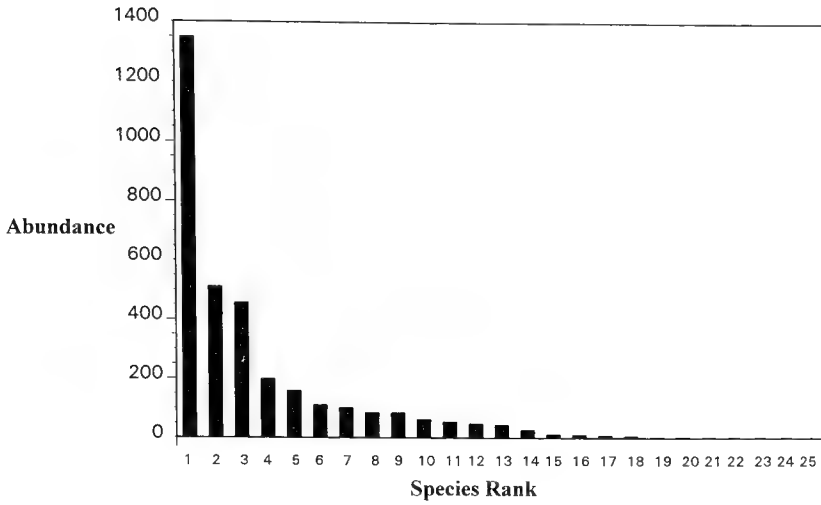


Figure 1. Ranked abundance of collembolan species collected.

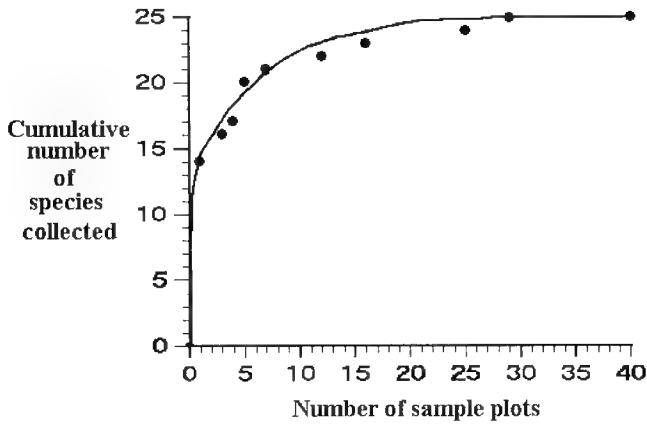


Figure 2. Species area curve for soil Collembola collected over 40 sample plots.

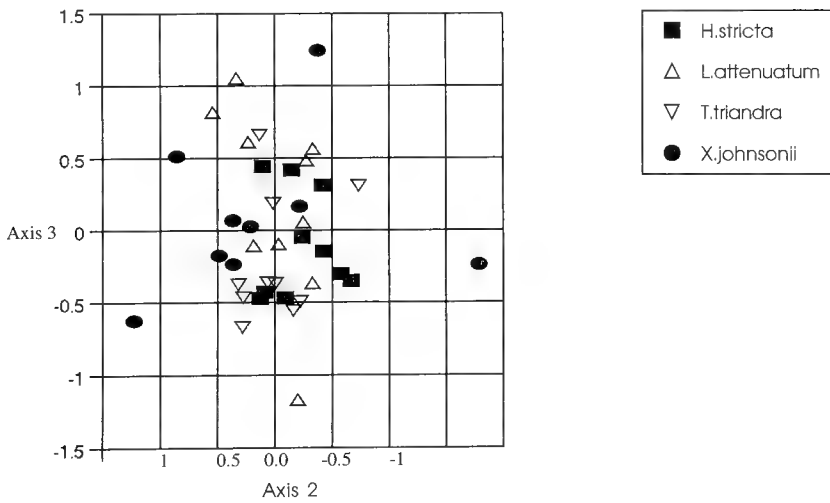


Figure 3. Ordination of collembolan assemblage dissimilarity, axes 2 and 3 (Semi-strong hybrid MDS, stress = 0.143, axes are unitless).

Since the dissimilarity coefficient quantifies the relationship between two sets of species data, quantification of the relationship between soil moisture contents of two plots was a necessary preliminary step to an analysis of the relationship between soil moisture and assemblage similarity. An exploratory 3-dimensional plot of assemblage dissimilarity against the soil moisture content of the two relevant plots, indicated that dissimilarity was low when two wet plots were compared, and high when wet and dry, or two dry plots were compared. Given the results of the soil moisture analyses in Table 3, it might be expected that dissimilarity in comparisons between *X. johnsonii* plots would be significantly higher than in comparisons between *H. stricta* plots. Tests of this hypothesis (Mann-Whitney U test) showed that dissimilarity was significantly higher in comparisons between *X. johnsonii* plots (the driest on the site) than in comparisons between *H. stricta* plots (the wettest on the site), for both species abundance and presence/absence data ($\alpha = 0.01$) ($Z = -3.06$ and -4.466 respectively).

The MDS plot (Figure 3), represents dissimilarity as distance between the points in the ordination space. The greater spread of *X. johnsonii* points in the figure is consistent with the higher level of dissimilarity between these plots than that between *H. stricta* plots. The distribution of the points in Figure 3 is also consistent with the conclusion that there is no significant structural difference between the assemblages associated with these two plant species.

The results of the above analyses provide justification further testing of the primary hypothesis. For example if soil moisture were controlled (i.e. by irrigation), then the points plotted in Figure 3 may condense to form tighter clusters. Whether or not the points for *X. johnsonii* and *H. stricta* would condense around the same centroid seems open to question. If some dissimilarity attributed to variation in soil moisture was controlled for in a more experimentally oriented study, then more subtle differences in collembolan assemblage structure associated with different plant species, such as the distribution of *Willowsia* sp., might increase in significance.

References

- Belbin, L., 1995. *PATN — pattern analysis package*. CSIRO, Division of Wildlife and Ecology: Lyneham ACT, Australia.
- Bowen, G.D. and Rovira, A.D., 1991. The rhizosphere, the hidden half of the hidden half. Pp. 641–669 in: Waisel, Eshel and Kafkafi (eds), *Plant roots, the hidden half*. Marcel Dekker Inc.: New York.
- Butcher, J.W., Snider, R. and Snider, R.J., 1971. Bioecology of edaphic Collembola and Acarina. *Annual Review of Entomology* 16: 249–288.
- Chapman, K., Whittaker, J.B. and Heal, O.W., 1988. Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agriculture Ecosystems and Environment* 24: 33–40.
- Curl, E.A. and Truelove, B., 1986. *The rhizosphere*. Springer-Verlag: New York.
- Coutts, R.H., 1987. Plant community descriptions (botanical analysis). Pp.165–171 in: Catterall, C.P. and Wallace, C.J. (eds), *An island in suburbia: the natural and social history of Toohey Forest*. Institute of Applied Environmental Research, Griffith University: Brisbane.
- Fjellberg, A., 1985. Recent advances and future needs in the study of Collembola biology and systematics. *Quaestiones Entomologicae* 21: 559–570.
- Foster, R.C., 1983. The plant root environment. Pp. 673–684 in: *Soils, an Australian viewpoint*. Division of Soils, CSIRO: Melbourne / Academic Press: London.
- Greenslade, P.J., 1991. Collembola (springtails). Pp. 252–264 in: *The insects of Australia: a textbook for students and research workers*. CSIRO, Division of Entomology / Melbourne University Press: Melbourne.
- Grubb, P.J. and Suter, M. B., 1970. The mechanism of acidification of soil by *Calluna* and *Ulex* and the significance for conservation. In: Duffey, E. and Watt, A. S. (eds), *The scientific management of animal and plant communities for conservation*. (11th Symposium of the British Ecological Society). Blackwell Scientific Publications: London.
- Hagvar, S., 1982. Collembola in Norwegian coniferous forest soils I. Relations to plant communities and soil fertility. *Pedobiologia* 24: 255–296.
- Hutson, B.R. and Veitch, L.G., 1983. Mean annual population density of Collembola and Acari in the soil and litter of three indigenous South Australian forests. *Australian Journal of Ecology* 8: 113–126.
- Hutson, B.R. and Veitch, L.G., 1987. Densities of Collembola and Acarina in the soil and litter of three indigenous South Australian forests related to layer, site and seasonal differences. *Australian Journal of Ecology* 12: 239–261.
- Klironomos, J.N., Widden, P. and Deslandes, I., 1992. Feeding preferences of the collembolan *Folsomia candida* in relation to microfungus successions on decaying litter. *Soil Biology and Biochemistry* 24(7): 685–692.
- Knight, C.B. and Read, V., 1969. Microstratification of *Tomocerus* (Collembola) in a pine-open field continuum. *Revue d'Ecologie et de Biologie du Sol* 1(2): 221–234.
- Mallik, M.A.B. and Tesfai, K., 1988. Allelopathic effect of common weeds on soybean growth and

- soybean-*Bradyrhizobium* symbiosis. *Plant Soil* 112: 177-182.
- Neill, R.L. and Rice, E. L., 1971. Possible role of *Ambrosia psilostachya* on pattern and succession in old-fields. *American Midland Naturalist* 86(2): 344-357.
- Plymouth Marine Laboratory. 1994. *PRIMER — Plymouth routines in multivariate ecological research*. Plymouth Marine Laboratory: Plymouth.
- Robinson, R.K., 1972. The production by roots of *Caluna vulgaris* of a factor inhibitory to growth of some mycorrhizal fungi. *Journal of Ecology* 60: 219-224.
- Shaw, P.J.A., 1985. Grazing preferences of *Onychiuris armatus* (Insecta: Collembola) for mycorrhizal and saprophytic fungi of pine plantations. Pp. 333-337 in: Fitter, A.H. (ed.), *Ecological interactions in soil plants, microbes and animals*. Blackwell Scientific Publications: London.
- Stock, E., 1987. Topography, geology and soils. Pp. 38-52 in: Catterall, C.P. and Wallace, C.J. (eds), *An island in suburbia: the natural and social history of Toohey Forest*. Institute of Applied Environmental Research, Griffith University: Brisbane.
- van der Drift, J., 1963. The disappearance of litter in mull and moor in connection with weather conditions and the activity of the macrofauna. Pp.125-133 in: Doeksen, J. and van der Drift, J. (eds), *Soil organisms*. North- Holland Publishing Company: Amsterdam.
- Vegter, J.J., 1983. Food and habitat specialisation in coexisting springtails (Collembola, Entomobryidae). *Pedobiologia* 25: 253-262.
- Verhoef, H.A. and Witteveen, J., 1980. Water balance in Collembola and its relation to habitat selection: cuticular water loss and uptake. *Journal of Insect Physiology* 26: 201-208.
- Weier, E.T., Stocking, C.R., Barbour, M.G. and Rost, T.L., 1982. *Botany: an introduction to plant biology*. John Wiley and Sons: Brisbane.
- Wiggins, E.A. and Curl, E.A., 1979. Interactions of Collembola and microflora of cotton rhizosphere. *Phytopathology* 69(3): 244-249.

SOIL INVERTEBRATE BIODIVERSITY IN STRINGYBARK FOREST IN THE NEW ENGLAND TABLELANDS BEFORE CLEARING

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Abstract

Lobry de Bruyn, L. A., Jenkins, B. A. and Sutrisno, 1997. Soil invertebrate biodiversity in stringybark forest in the New England tablelands before clearing. *Memoirs of the Museum of Victoria* 56 (2): 295–303.

In this study at Newholme, 10 km N of Armidale, in northern New South Wales, we will assess the role of soil invertebrates as ecosystem engineers after a major disturbance — clearing of native vegetation for grazing pastures. The data presented in this paper is from the December 1993 pitfall trapping prior to clearing. The pitfall trapping recorded 22 invertebrate groups, dominated by eight, with Collembola, Acarina and Formicidae being the most abundant groups. Formicidae was further classified into species which revealed the average site had 24 species of ants, and in total there were 57 ant species recorded over 12 sites. Those sites with high ant abundance were dominated by one or more of the following three ant species: *Aphaenogaster* sp. N26, *Iridomyrmex* sp. N60, or *Pheidole* sp. N2. The dominant ant functional group in abundance and number of species was the Climate/Soil Specialist. The following functional groups, in order of declining abundance, were Dominant dolichoderinae, Generalised myrmicines and Opportunists, and were all represented by at the most four species. The remaining functional groups were low in abundance and recorded low species richness, which may be a reflection of trapability rather than reality.

Introduction

In examining the extent of land degradation in Australia one becomes immediately aware of the enormity of the problem, especially in agricultural soils. Solutions to land degradation often revolve around retention or replanting of native or introduced tree species, but minor consideration is given to their interactions with other parameters. The integral role of soil invertebrates in maintaining soil fertility (physical and chemical) is often overlooked. Also there has been little evaluation of the role of soil invertebrates in restoring degraded soils through their input into soil processes. Most of the epigeic soil invertebrates sampled by pitfall trapping (such as ants, beetles, spiders, Araneae and Collembola) do interact with other soil biota and soil properties, and make a significant contribution to nutrient cycling and the maintenance of soil structural properties. The impact of soil fauna on soil processes which include nutrient cycling, soil bioturbation and soil structure formation (Hole, 1981) have only been examined, in part, by a small selection of studies in Australia (Lobry de Bruyn, 1990; Mitchell, 1986; Humphreys, 1985). Research overseas has been more extensive, but has concentrated on earthworm species (Kretzschmar, 1992; Brussaard and

Kooistra, 1993) or termite species, usually not known to occur in Australia. A review of the overseas and Australian literature on the role of termites and ants in soil modification (Lobry de Bruyn and Conacher, 1990) emphasised the lack of data on ant-soil relationships as well as subterranean termites and soil processes.

In this study at Newholme (10 km N of Armidale in northern New South Wales) we will identify key soil invertebrate groups, which are present in the Stringybark Forest. This forest will then be converted to grazing land (with two levels of tree cover) which we assume will simplify the soil ecosystem, both structurally and functionally. We hope to ascertain which invertebrate groups are lost, persist or increase in abundance in this changed environment, and whether functional diversity is reduced because of ecosystem simplification. The overall aim is to assess the role of soil invertebrates as ecosystem engineers by examining their function in the maintenance of soil structure processes after a major disturbance — clearing of native vegetation for grazing pastures. The term ecosystem engineers is taken from Jones and Lawton (1995) and they describe ecosystem engineers as “organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or

abiotic materials. In doing so they modify, maintain, and/or create habitats." To decide which organisms hold this role in the predisturbance state a series of pitfall trapping combined with mapping was undertaken in December 1993, February 1994 and September 1994. The baseline survey will identify soil invertebrate composition and abundance prior to clearing, establish inter-site variability, soil invertebrate species abundance and activity, and the spatial distribution in the landscape of soil invertebrate species activity. At this stage this paper will report on the December 1993 pitfall trapping data, examining ordinal, ant functional and ant species biodiversity.

Methods

The activity and nest density of soil macrofauna (principally ants, termites, earthworms and spiders) were sampled by a combination of pitfall trapping, soil sampling and mapping (Lobry de Bruyn, 1993a, b). Three baseline pitfall trapping sampling periods were completed prior to clearing (13–20 Dec 1993, 16–23 Feb 1994, and 14–24 Sep 1994). This paper will report only on the pitfall sampling data taken in December 1993, since this is the only sampling period where the ants have been sorted to species. Weather conditions during the December pitfall trapping week were fine and hot with an average minimum daily temperature of 11.8°C and a maximum daily temperature of 29.5°C. There was only one minor rainfall event of 3 mm on 16 Dec 1993, and on the whole the days were cloudless.

Each site is 4 ha. Plots within these sites have been chosen which are all beneath trees, in the mid-slope position, except site E, and on a grey podzolic soil. These sites will be subject to varying patterns of tree removal and fertiliser amendments as well as use of sub-clover. The treatments that will be imposed are as follows:

1. control — retain trees unamended (A, H, L)
2. control — retain trees plus add fertiliser/sub-clover (D, E, I)
3. thinning + fertiliser/sub-clover (C, G, K)
4. clearfell + fertiliser/sub-clover (B, F, J)

The foraging activity of invertebrates was recorded with 20 pitfall traps per plot (40 × 50 m), with one pitfall trap placed randomly within a 10 × 10 m quadrat. There were a total of 240 pitfall traps/sampling period. The pitfall traps were left open for a week, and were 4.5 cm

in diameter. They were filled with 70% alcohol and 10% glycerol.

To assist in interpretation of ant biodiversity, the functional groups approach used by Andersen (1990) to document mine restoration success was employed (Andersen, 1993). Greenslade and Greenslade (1984) developed the functional group classification based on habitat and competitive interactions with *Iridomyrmex*. There are seven functional groups into which various genera can be classified. The most important group is the dominant dolichoderinae which is dominated by *Iridomyrmex* sp. These ants are considered to be highly abundant, active and aggressive and strongly influence the presence of other ant species. They predominate in open habitats, with high soil temperatures and where the soil surface is not covered with litter. The remaining functional groups occur in habitats either not favoured by *Iridomyrmex* sp. or have specialisations reducing their interaction with this species. Andersen (1990) sees the group of ant genera such as *Rhytidoponera* sp. which fall into the Opportunists functional group as important indicators of a disturbed site or a site low in *Iridomyrmex* sp. numbers. This group is usually poorly competitive and unspecialised.

Results and discussion

In total there were 22 invertebrate groups, with 11 orders on average recorded per pitfall trap. The most abundant invertebrate groups from all sites, in decreasing order of abundance were, Collembola (1063 per pitfall trap), Acarina (80 per pitfall trap), Formicidae (58 per pitfall trap), Diptera (20 per pitfall trap), Coleoptera (17 per pitfall trap), Hymenoptera (12 per pitfall trap), Araneae (5 per pitfall trap), Hemiptera (4 per pitfall trap) and Dermaptera (1 per pitfall trap) (Fig. 1, Collembola were excluded from the figure because of their high abundance). The remaining invertebrate groups recorded on average less than one specimen per pitfall trap.

A One-Way ANOVA of log transformed data ($\log_{10}x + 1$) showed no significant differences in invertebrate abundance between sites for the Araneae, Acarina, and Coleoptera. The two invertebrate groups which were the most variable in abundance were Formicidae and Collembola. It appears that sites B and D, have a lower abundance of ants than most sites, especially sites G, H, K and L ($p < 0.001$) (Appendix 1). However, a significantly higher abundance of ants was recorded for Sites K and L compared

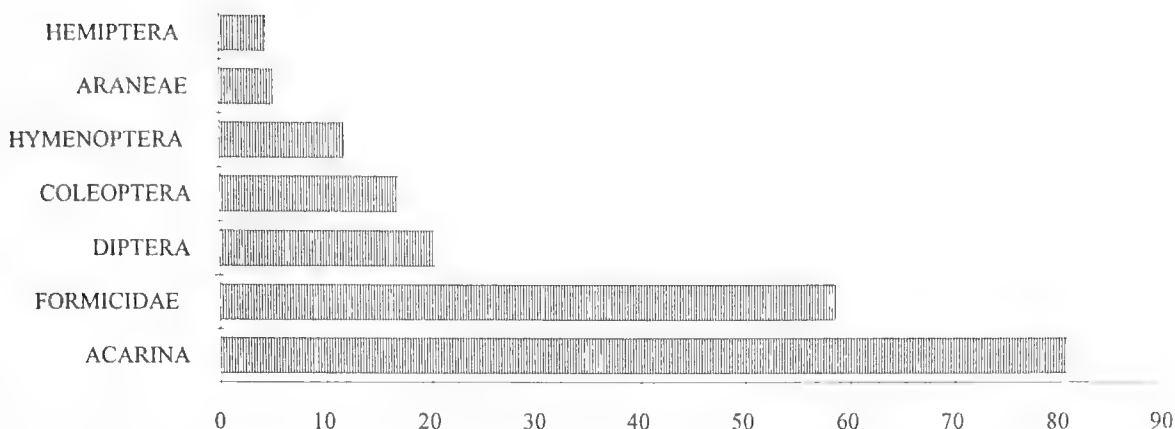


Figure 1. Invertebrate biodiversity at the order level, except for Formicidae, for the average site in December 1993 ($n=12$ sites). Collembola are excluded due to their high abundance.

with Sites G and H ($p < 0.001$) (Appendix 1). Numbers of Araneae were low but the pitfall trap catch number is consistent across the various sites. In contrast Formicidae abundance coefficient of variability (CV) increased from 1.1 (for sites A to D) to 2.2 (when all 12 sites were examined) in December 1993 indicating a patchy distribution. Sites B and C have significantly lower abundances of Collembola compared with all other sites ($0.0001 > p < 0.01$). Interestingly with the further analysis of data the CV for Collembola declined from 3.1 (only for four sites) to 2.6 (all 12 sites), similarly the CV for Coleoptera abundances declined from 2.2 to 1.6 indicating a less patchy distribution than first surmised.

Of the invertebrate groups identified in the baseline survey in December 1993 which groups have an important ecosystem function, especially in relation to soil modification? At this stage the December survey has identified three important ecosystem engineers. Collembola and Araneae, the two most abundant orders, would contribute to nutrient cycling by regulating microbial communities which are responsible for 90% of organic carbon turnover. The ants, the third most abundant invertebrate group, carry out a series of important ecosystem functions. Past research in the wheatbelt of Western Australia in a woodland environment (Lobry de Bruyn and Conacher, 1994a, b), has indicated ants perform important roles in soil mixing and water infiltration under ponded conditions.

The implication of the spatial variability in abundance of some invertebrate groups between

sites will have important implications once the treatments are imposed, and the realisation that the natural variability of each site may be greater than the treatment effect. Consideration to the variability between sites will also need to be given at the stage of data analysis and interpretation. Three of the six sites which are to be affected by tree removal have significantly higher numbers of ants, while one of these sites has much lower numbers of ants than the other sites. Also two sites (one which will be modified) have much lower levels of Collembola numbers than the remaining ten sites. The ant data was examined further to see if those sites with greater ant abundance also varied markedly in ant species richness or were composed of a different suite of ant functional groups to the other sites.

The average site recorded almost equal proportions (around 30%) of three functional groups: dominant Dolichoderinae, generalised myrmicines, and opportunists. The remaining four functional groups accounted for just over 10% of the remaining ant numbers, with the majority recorded as climate/soil specialists (Fig. 2).

The low numbers of subordinate Formicinae dominated by the genera *Camponotus* sp. was unexpected considering the woodland habitat. The low numbers of catches for subordinate Formicinae, cryptic species and specialist predators may be influenced by their trapability. Those sites with higher numbers of ants were dominated by one of the following three ant species. At site L, *Aphaenogaster* sp. N26 dominated, at site F *Pheidole* sp. N2, at site K, *Iridomyrmex* sp.

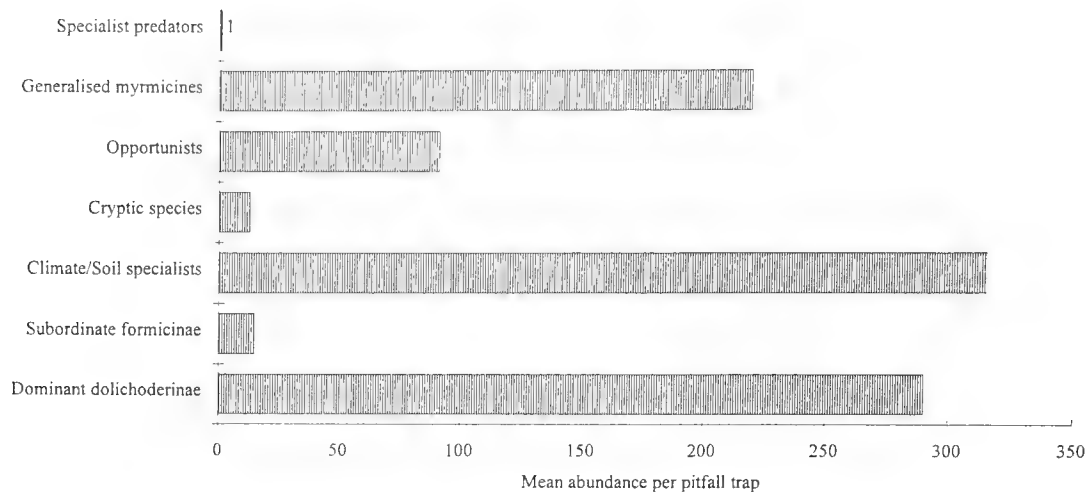


Figure 2. Abundance of ants recorded in each of the ant functional groups at an average site (n=12 sites, 20 pitfall traps per site) in December 1993.

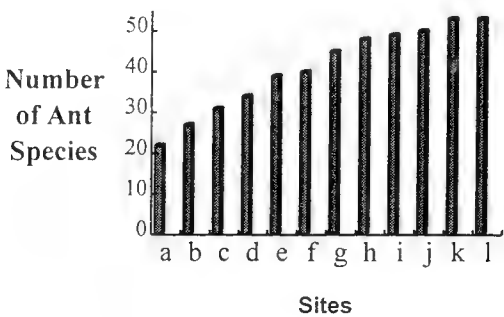


Figure 3. The ant species accumulation curve for sites A to L in December 1993.

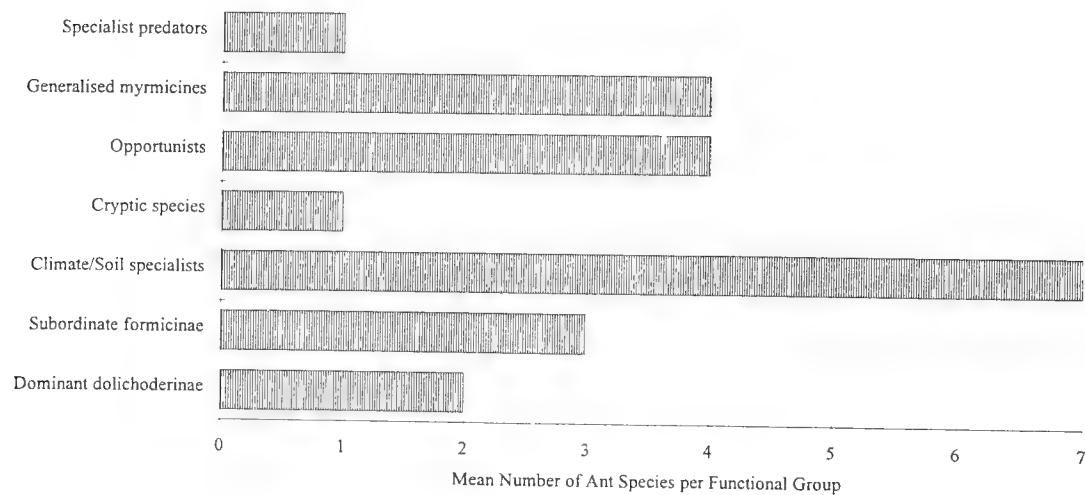


Figure 4. Number of ants species recorded in each of the ant functional groups at an average site (n=12 sites, 20 pitfall traps per site) in December 1993.

N60, and at site G a combination of equally high numbers of *Aphaenogaster* sp. N26 and *Iridomyrmex* sp. N60. On the other hand, sites B and D, which had low ant abundance recorded below average numbers of *Aphaenogaster* sp. N26, *Pheidole* sp. N2, and *Iridomyrmex* sp. N60.

The total number of ant species over all sites in December 1993 was 53 species. There was an average of 22 species of ant per site, ranging from 15 to 28 ant species. Figure 3 shows the accumulation of species per site. More than half the ant species were recorded in sites A and B, with the addition of two to three species in each of the following 10 sites. The new species recorded were often represented by a few specimens (Appendix 2).

The proportion of species in each functional group for an average site is shown in Figure 4. The most species rich ant functional groups were the climate/soil specialists, predominantly *Aphaenogaster* sp. N26 (soil), *Notoncus* spp., and *Prolasius* spp. (both climate), with seven species. While the opportunists (predominantly four species of *Rhytidoponera* spp., mostly *Rhytidoponera metallica*), subordinate formicinae and the generalised myrmicines were all represented by four species each. The other three functional groups (cryptic species, specialist predators and dominant Dolichoderinae) had on average less than two species per site each. Interestingly the sites with the highest ant numbers also had the greatest number of ant species and vice versa.

The sort of changes expected with clearing include a more open canopy, higher soil temperatures and less litter. Hence, in future pitfall trapping, an increase in *Iridomyrmex* spp. and a decline in *Aphaenogaster* sp. N26 abundance might be expected. There may also be an increase in numbers of some of the *Pheidole* spp. In terms of soil mixing *Aphaenogaster* sp. N26 is the most prominent nest-builder and has a very aggregated nest distribution. On average *Aphaenogaster* sp. N26 nest density was in the order of 10 nests m⁻² (unpublished data). The decline of this species could severely disrupt soil forming processes, and the movement of water under high energy rainfall events. *Aphaenogaster* sp. N26 has specialised feeding habits (Davison pers comm. 1995) and a preference for sandier textured soils (Lobry de Bruyn and Conacher 1994a) which may explain the aggregated and patchy nature of *Aphaenogaster* sp. N26 nests. However more work is needed to determine the influence of these factors on nest density and spatial patterning.

Acknowledgements

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References

- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a recipe and a review. *Proceedings of the Ecological Society of Australia* 16: 347–357.
- Andersen, A.N., 1993. Ants as indicators of restoration success at a uranium mine in tropical Australia. *Restoration Ecology* 1: 156–167.
- Brussaard, L., and Kooistra, M.J. (eds), 1993. International Workshop on Methods of Research on Soil Structure/Soil Biota Interrelationships — Wageningen, The Netherlands 24–28 November 1991. *Geoderma* 56–57.
- Greenslade, P.J.M., and Greenslade, P., 1984. Soil surface insects of the Australian arid zone. Pp 153–176. in: Cogger, H.G. and Cameron, E.E. (eds). *Arid Australia*. Australian Museum: Sydney.
- Hole, F.D., 1981. Effects of animals on soil. *Geoderma* 25: 75–112.
- Humphreys, G.S., 1985. *Bioturbation, rainwash and texture contrast soils — an evaluation of transporting processes on soil genesis in the Sydney Basin*. PhD thesis, Macquarie University, Sydney.
- Jones, C.G. and Lawton, J.H. (eds), 1995. *Linking species and ecosystems*. Chapman and Hall: London.
- Kretzschmar, A., (ed.), 1992. 4th International Symposium on Earthworm Ecology — Avignon, France, 11–15 June 1990 *Soil Biology and Biochemistry* 24: 1193–1773.
- Lobry de Bruyn, L. A., 1990. *The role of ants and termites in modifying soil properties in naturally vegetated and agricultural environments*. PhD thesis, University of WA, Nedlands.
- Lobry de Bruyn, L. A., 1993a. Defining soil macrofauna composition and activity for biopedological studies: a case study on two soils in the Western Australian wheatbelt. *Australian Journal of Soil Research* 31: 83–95.
- Lobry de Bruyn, L.A., 1993b. Ant composition and activity in naturally vegetated and farmland environments on contrasting soils at Kellerberrin, Western Australia. *Soil Biology and Biochemistry* 25: 1043–1056.
- Lobry de Bruyn, L. A., and Conacher, A. J., 1990. The role of termites and ants in soil modification: a review. *Australian Journal of Soil Research* 28: 55–93.
- Lobry de Bruyn, L. A. and Conacher, A. J., 1994a. The effect of ant biopores on water infiltration in soils in undisturbed bushland and in farmland in a semi-arid environment. *Pedobiologia* 38: 193–207.

- Lobry de Bruyn, L. A. and Conacher, A. J., 1994b. The bioturbation activity of ants in agricultural and naturally vegetated habitats in semi-arid environments. *Australian Journal of Soil Research* 32: 555-570.
- Mitchell, P. B., 1986. *Some aspects of the role of bioturbation in soil formation in south eastern Australia*. PhD thesis, Macquarie University, Sydney.

Appendix 1: Average catch per pitfall trap for all invertebrate orders and ants in a Temperate Stringybark Forest in December 1993

	SITE A		SITE B		SITE C		SITE D		SITE E		SITE F		SITE G		SITE H		SITE I		SITE J		SITE K		SITE L	
	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE
ORDERS	71.10	12.94	88.85	30.15	53.60	6.73	38.17	6.32	110.16	20.51	76.10	13.70	84.00	10.18	71.72	9.07	97.72	13.20	105.19	11.76	74.00	10.36	95.75	19.36
ACARINA	3.95	0.52	3.45	0.48	3.05	0.46	3.83	0.58	5.74	0.63	3.40	0.44	5.30	0.65	6.61	0.61	6.00	0.89	8.44	1.79	4.26	0.62	6.25	0.80
ARANEAE	12.95	1.66	26.25	15.51	14.30	2.09	10.44	1.25	13.74	1.88	17.90	1.99	14.40	2.44	23.39	2.48	16.33	2.65	21.56	3.74	18.47	2.22	11.60	2.12
COLEOPTERA	1170.3	678.2	203.3	47.9	103.2	11.2	777.9	309.7	1107.2	332.0	444.2	67.6	1017.7	558.0	1430.6	782.2	1439.9	433.4	2163.6	1204.8	2555.3	1300.6	342.0	100.0
COLLEMBOLA	8.45	1.27	3.15	1.25	0.85	0.36	0.89	0.40	0.05	0.05	0.20	0.20	0.00	0.00	0.00	0.00	0.11	0.11	0.13	0.09	0.00	0.00	0.05	0.05
DERMAPTERA	20.00	2.33	28.00	6.14	38.45	8.24	32.56	4.60	11.11	1.53	13.80	1.43	16.60	2.15	20.61	3.09	11.56	2.09	16.13	3.54	16.05	1.90	18.35	2.34
DIPTERA	48.55	15.03	28.45	4.92	45.30	6.81	18.11	2.46	44.47	5.14	75.40	22.62	72.15	15.26	44.44	6.74	79.61	35.28	47.19	9.12	68.95	8.75	129.65	70.76
FORMICIDAE	10.74	5.29	3.70	0.81	5.50	0.84	2.89	0.41	4.06	0.74	5.60	1.36	4.40	0.58	3.67	0.50	2.53	0.48	2.88	0.50	3.26	0.55	3.30	0.53
HEMiptERA	9.90	0.95	9.20	1.61	17.05	1.52	15.33	1.61	9.58	1.10	12.40	1.61	11.10	1.30	12.11	1.09	8.72	1.08	14.00	1.58	11.16	1.23	10.20	1.02
HYMENOPTERA	0.74	0.18	0.30	0.13	0.45	0.14	0.39	0.14	0.95	0.05	0.05	0.05	0.10	0.07	0.11	0.08	0.22	0.10	0.19	0.10	0.15	0.05	0.10	0.07
LEPIDOPTERA	0.10	0.07	1.00	0.42	0.95	0.28	0.39	0.12	0.00	0.00	0.30	0.13	0.30	0.11	0.22	0.10	0.22	0.10	0.75	0.28	0.11	0.07	0.15	0.15
ORTHOPTERA	0.50	0.21	0.00	0.00	0.20	0.09	0.50	0.35	0.00	0.00	0.10	0.07	1.40	0.84	0.39	0.14	0.22	0.17	0.44	0.18	0.16	0.09	0.10	0.07
PSOCOPTERA	1.25	0.47	0.85	0.23	0.84	0.24	1.06	0.41	0.89	0.24	1.40	0.28	0.75	0.19	0.61	0.16	0.56	0.18	0.63	0.24	0.53	0.30	0.90	0.22
THYSANOPTERA	1.15	0.35	1.30	0.48	1.00	0.30	0.61	0.27	3.16	1.75	1.15	0.25	1.35	0.47	2.00	0.67	1.28	0.27	2.31	0.79	0.42	0.16	1.00	0.33
LARVAE	0.65	0.17	0.60	0.21	0.65	0.25	0.61	0.22	0.74	0.23	0.40	0.13	0.25	0.12	0.94	0.22	0.22	0.10	0.88	0.31	0.58	0.16	0.70	0.21
BLATTEODA	0.10	0.13	0.20	0.12	0.25	0.14	0.17	0.12	0.53	0.38	0.10	0.07	0.15	0.08	0.33	0.14	0.17	0.09	0.25	0.11	0.00	0.00	0.05	0.05
DIPLOPODA	0.30	0.05	0.15	0.08	0.10	0.07	0.61	0.26	0.32	0.15	0.20	0.09	0.25	0.16	0.50	0.17	0.28	0.14	0.56	0.26	0.00	0.00	0.05	0.05
ISOPODA	0.05	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
MANITOEDA	0.00	0.00	0.05	0.05	0.15	0.08	0.11	0.08	0.05	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CHILPODA	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
NEUROPTERA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ISOPTERA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
THYSANURA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.00	0.00	0.00
THYSANURA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
DIPLURA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PSEUDOSCORPION	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.05	0.00	0.00	0.00	0.00	0.11	0.08	0.06	0.06	0.00	0.00	0.00	0.00
AMPHIPODA	0.00	0.00	0.00	0.00	0.00	0.05	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 2. Total Abundance of Ant Species Classified into Functional Groups in Temperate Stringybark Forest in December 1993.

Dec-93 SPECIES	site a total	site b total	site c total	site d total	site e total	site f total	site g total	site h total	site i total	site j total	site k total	site l total	total	SE
1. Dominant dolichoderinae														
<i>Iridomyrmex (discors gp.) sp. N1</i>	80	48	93	3	17	34	15	14	4	29	1	89		
<i>Ochetellus sp. N46</i>	19		3		5				16	6		5		
<i>Iridomyrmex sp. N60</i>		74	50	63	81	340	521	170	815	136	524	223		
total abundance	99	122	146	66	103	374	536	184	835	171	525	317	290	68
no of species	2	2	3	2	3	2	2	2	3	3	2	3	2	
2. Subordinate formicinae														
<i>Camponotus sp. N7</i>	19	8	2	3	5	2	3	3	2		7	8		
<i>Camponotus sp. N44</i>					9	7	1	1		6	1	1		
<i>Camponotus sp. N54</i>	1		1				3		12	8	1			
<i>Camponotus sp. N75</i>					2		7	8	3	4	29			
<i>Camponotus sp. N76</i>						2		1	1					
<i>Camponotus sp. N92</i>										7				
<i>Polyrhachis sp. N45</i>	1													
<i>Polyrhachis sp. N77</i>							1							
<i>Polyrhachis sp. N80</i>							1							
<i>Polyrhachis sp. N83</i>							1							
total abundance	21	8	3	3	16	11	17	13	18	25	38	9	15	3
no of species	3	1	2	1	3	3	7	4	4	4	4	2	3	
3. Climatic/Soil Specialists														
<i>Aphaenogaster sp. N26</i>	203	165	279	58	385	92	601	187	261	234	85	560		
<i>Leptomyrmex sp. N12</i>				2	2		2	3	1		2	1		
<i>Dolichoderus sp. N 55</i>	3									2	2			
<i>Dolichoderus sp. N 57</i>	1			5					8					
<i>Melophorus sp. N64</i>	4					12	11			6	6	45		
<i>Melophorus sp. N65</i>			9	2	1	1	1							
<i>Melophorus sp. N66</i>			7		3		12		4	2		20		
<i>Meranoplus sp. N10</i>	3	6		1	11	16	17	12	5	5	25	38		
<i>Notoncus sp. N43</i>	33		78	8	8		9	18	6	8	21	7		
<i>Notoncus sp. N58</i>		10							1			10		
<i>Prolasius sp. N59</i>	4	13	21	9	13	11	7	17	11	6	2	16		
total abundance	251	194	394	85	423	132	660	237	297	263	143	697	315	57
no of species	7	4	5	7	7	5	8	5	8	7	7	8	7	
4. Cryptic Species														
<i>Amblypone sp. N74</i>					1		1							
<i>Brachyponera sp. N53</i>	2			1						1		4		
<i>Sphinctomyrmex sp. N71</i>					6	3	3				1			
<i>Sphinctomyrmex sp. N73</i>					4	13	14		4			94		
<i>Stigmatoceros sp. N91</i>											1			
total abundance	2	0	0	1	11	16	18	0	4	1	2	98	13	8
no of species	1	0	0	1	3	2	3	0	1	1	2	2	1	

Appendix 2 Continued

Dec-93 SPECIES	site a total	site b total	site c total	site d total	site e total	site f total	site g total	site h total	site i total	site j total	site k total	site l total	total	SE
5. Opportunists														
<i>Paratrechina</i> sp. N42	15	92	7		30	18	11		1		156	41		
<i>Paratrechina</i> sp. N62			2											
<i>Rhytidoponera</i> sp. N15	4	24	2	1		12			2		13			
<i>Rhytidoponera</i> sp. N4	13	39	32	26	29	10		17	36	33	57	30		
<i>Rhytidoponera</i> sp. N23											1			
<i>Rhytidoponera</i> sp. N50	8		5	12	4	2		1	4	7	2			
<i>Rhytidoponera</i> sp. N61		6												
<i>Tapinoma</i> sp. N20		5	2		70	25	6		61	58	46			
<i>Tetramorium</i> sp. N18		2			2						6	2		
total abundance	40	168	50	39	135	67	17	18	104	98	281	73	91	22
no of species	4	6	6	3	5	5	2	2	5	3	7	3	4	
6. Generalised myrmicines														
<i>Crematogaster</i> sp. N72					12	5		38		30	25			
<i>Solenopsis</i> sp. N3	2			3	8	64	25	17	21		10			
<i>Monomorium</i> sp. N16	52	7				10	6			4	4			
<i>Monomorium</i> sp. N85								2						
<i>Monomorium</i> sp. N90											4	5		
<i>Pheidole</i> sp. N2	420	82	246	38	63	445	29	42	135	28	112	39		
<i>Pheidole</i> sp. N69				34	42	225	57	131	17	17	33	29		
<i>Pheidole</i> sp. N81							10							
total abundance	474	89	246	75	125	749	127	230	173	79	188	73	219	58
no of species	3	2	1	3	4	5	5	5	3	4	6	3	4	
7. Specialist predators														
<i>Cerapachys</i> sp. N84								2						
<i>Myrmecia</i> sp. N70				1	5									
<i>Myrmecia</i> sp. N88									2			1		
<i>Myrmecia mandibularis</i>								1						
total abundance	0	0	0	1	5	0	0	1	2	0	0	1	1	0.40
no of species	0	0	0	1	1	0	0	2	1	0	0	1	1	
total abundance	887	581	839	270	818	1349	1375	683	1433	637	1177	1268	943	107
total no of species	20	15	17	18	26	22	27	20	25	22	28	22	22	

SHORT TERM EFFECTS OF A PRESCRIBED BURN ON INVERTEBRATES IN GRASSY WOODLAND IN SOUTH-EASTERN AUSTRALIA

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Abstract

Greenslade, P., 1997. Short term effects of a prescribed burn on invertebrates in grassy woodland in south-eastern Australia. *Memoirs of the Museum of Victoria* 56(2): 305-312.

The effect of fire on invertebrates in a remnant undisturbed white box woodland with a *Themeda* understorey is reported. The woodland was burnt experimentally in May 1994 with half the plots fenced against grazing. Invertebrates were sampled every four months for 16 months using a suction sampler. Initially, lower numbers of invertebrate individuals were collected on the burnt compared with the unburnt plots but after sixteen months this difference had disappeared for all higher taxa. However there were differences in composition of collembolan fauna and relative abundance of species caught between burnt and unburnt plots and between fenced and unfenced plots.

Introduction

Although some Australian plant communities are adapted to fire, the frequency, timing and intensity of burning influences the rate of recovery of structure and function to the prefire state (Cheal, 1996; Tolhurst, 1996). Too frequent fires or a total absence of fire are both likely to result in loss of species and for each community type, the interval between burns which is optimum for sustainability will differ (Gill, 1996). In some plant communities there is evidence to suggest that the altered intensity and frequency of burning since European settlement is affecting invertebrate abundance and even causing local extinctions (York, 1996; Lowe, 1995). Alternatively in grasslands, the absence of fire may be reducing floristic diversity (Prober 1995). It may also affect invertebrates dependant on early successional plants for food or shelter.

The aim of most fuel reduction burning is to reduce the risk of wildfire, so the optimal conditions required for different plant communities are not usually considered (Gill, 1996). It is now increasingly recognised however, that fire management plans should be based on knowledge of the responses of all components of the fauna and flora to burning, so that as much of the biodiversity of the ecosystem as possible can be preserved (Anon, 1992). Fire management plans which protect floristic diversity and vegetation type will not necessarily protect invertebrate diversity, since invertebrates respond to abiotic factors differently from plants. They are also an order of magnitude more diverse, so larger num-

ber of species exhibit small scales of distribution. Cho et al. (1995), in a report on Jervis Bay National Park, NSW, state "the assumption that if all habitats are conserved then all invertebrates are conserved is generally well founded" and quote Nadoly (1984). However this assumption has been shown by a number of studies to be false (Greenslade and New, 1991 and included references). Until the invertebrate fauna has been surveyed and macro and microhabitats requirements determined, any fire management plan based on vegetation communities alone cannot guarantee to conserve the invertebrate fauna.

A review of previous work on fire and invertebrates has been published by Friend (1996) and more recently discussed by Greenslade et al. (1996). In many studies on effects of wild fires and prescribed burns on invertebrates in Australia, identification has been to the level of order (Neumann and Tollhurst, 1991; Abbott, 1984; Coy, 1996; Hutson and Kirkby, 1985) and these studies have tended to show a rapid recovery in abundance and representation of all orders after fire. Moreover some studies indicated that invertebrate responses to season and site were greater than to the fire itself (Friend, 1996). Consequently some authors have concluded that the effect on invertebrates of prescribed burning is short term and insignificant (Abbott et al., 1984; Neumann and Tollhurst, 1991).

A high proportion of the studies have been on ants (Majer, 1980; Andersen and Yen, 1985), a group which generally has a preference for open habitats and high temperatures so are favoured

by fire, which is not typical of the responses of invertebrates of more humid habitats to fire. Other higher taxa which could be appropriate "indicators" of fire effects were recommended by Friend (1996) in a review of research on fire and invertebrates in Australia. He concluded that five higher taxa were "sensitive to fire". These were Araneae, Lepidoptera, Isopoda, Blattodea and Thysanura. However Blattodea, Thysanura and Isopoda are not usually present in high enough numbers for data on them to be sufficiently informative, the taxonomic difficulties and high diversity of Araneae make their use as an "indicator group" problematical and the problems in sampling Lepidoptera quantitatively are well known. Greenslade and Rosser (1984) and Coy (1996) showed that Dermaptera and Amphipoda respectively were very sensitive to fire in having high abundances before burning and not having returned for a year after the burn. Where present, they are clearly taxa to be considered as candidates for "indicators."

Fire can also effect decomposition processes. For instance, by reducing populations of litter decomposing invertebrates fire can, even in the short term, result in a more rapid build up of fuel after a prescribed burn because of reduced rates of decomposition. Hodda (1991) found fewer and smaller harvester termite mounds in annually burnt areas compared to unburnt areas at Kakadu and in annually burnt areas there was also a reduced loss of leaf litter compared to unburnt areas and this was directly linked to a slower rate of removal of plant material by termite.

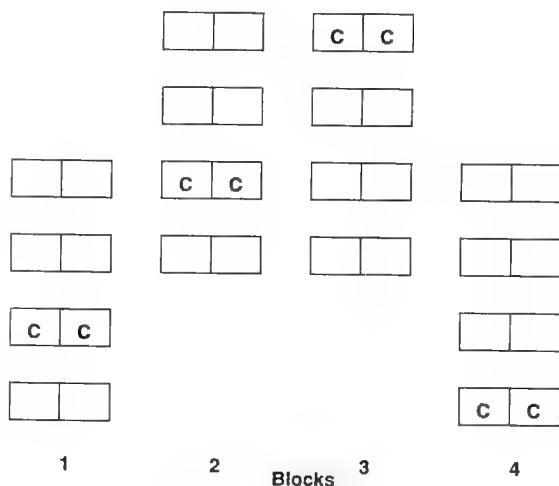
It has been shown that species composition of faunas from plant communities of different ages since fire can differ markedly (Friend and Williams, 1993 — beetles; Little and Friend, 1993 — spiders; Abensperg-Traun and Milewski, 1995 — termites; Hodda, 1991 — termites; Greenslade, 1994a — springtails) and that these differences in composition can persist for many years after the fire. Moreover there is some evidence to show that inappropriate fire regimes can cause local extinction of some species. One example is Leichhardt's grasshopper, *Petasida ephippigera* in Kakadu National Park (Low 1995) and in eucalypt forest north of Sydney, Alan York (1994, 1996) has shown that there is a suite of fire sensitive ant species which are lost from areas under an intensive burning regime. It is clear therefore that it is essential to identify the fauna to species and morphospecies to adequately demonstrate the

real effect of fire on invertebrate communities.

Most work on fire and invertebrates in Australia has been carried out in eucalypt woodland and forest. There has only been one previous study in grassland (Greenslade, 1994b). Here we identify the most abundant group collected, the Collembola, to species and in another study of fire in coastal heath (Greenslade et al., 1996) the total fauna was identified to morphospecies.

Site description

Woodstock cemetery, 33°45'S, 148°51'E, 20 km E of Cowra, NSW, is an isolated remnant patch of white box woodland with a dense understorey dominated by *Themeda* grassland. This site had never been cleared and had not been mown, grazed by stock or burnt for over 50 years. It is floristically diverse with 66 native vascular plants having been recorded from it (Prober and Thiele, pers. comm.) In 1994 an experimental site was established within the remnant by botanists from CSIRO Division of Plant Industry (Fig. 1) with the aim of investigating responses of plant species richness of the ground layer to fire. The total area of the remnant vegetation was about 5 hectares.



C = control plots. All other plots were burnt.

Figure 1. Details of experimental layout at Woodstock (after Prober, 1995). Each plot is 5 × 5 m. One of each pair is fenced. Adjacent pairs of plots are separated by a 5 m strip. The area between pairs of plots was slashed before burning.

Experimental design

In order to study fire effects on invertebrates, field experimentation is necessary. However if experimental plots are large enough to simulate natural conditions, site differences can swamp treatment differences (Friend and Williams, 1993; Friend, 1996). Alternatively if small plots are used to reduce variability and provide good replication so that fire effects can be measured independently of site variability, edge effects may influence faunal responses. An alternative method could be achieved by a nested plot design but practical problems made this impossible here. At Woodstock small, well replicated plots were used to study short term effects of an environmental burn on invertebrates in grassy white box woodland and in an alternative study large plots were used to study effects of a wildfire in coastal heathland and results from it are reported elsewhere (Greenslade et al., 1996).

A uniform area of just under 100 m by 100 m which sloped gently to the south and where trees were largely absent, was selected and divided into sixteen small plots, 5 m by 10 m, the blocks being separated by a 5 m wide strip. Half of each plot was fenced to prevent grazing by kangaroos and rabbits (Fig. 1). Suction sampling was used to survey the invertebrate fauna associated with the ground vegetation within the small plots at this site. The suction sampler used has been shown to take samples which are representative of the fauna present, are reproducible and semi-quantitative (Greenslade, 1994a). Two prefire samples were taken comprising sixteen samples each, one from each main plot, in spring (Nov 1993) and early autumn (1994), just prior to burning. All sampling was carried out between midday and 3 pm. Four post fire samples were taken, one from the unfenced plots at two months post burn and two from each main plot inside and outside the fence, at 5, 10 and 16 months after the burn. The fenced plots were not sampled until five months after burning as effects of grazing were unlikely to be evident earlier. Rainfall was well below average prior to all postfire sampling periods except the last two. Invertebrates were sorted to order and counted. The majority of specimens collected were Collembola which were identified to species. Other taxa were not present in sufficient numbers in the suction samples to be analysed at species level.

Burning

Twelve of the plots were burnt on 14 May 1994. The areas between plots and for a distance of about 5 m around the whole experimental area were dampened to confine burning to the plots themselves. Burning was carried out from the ground with a hand held flame torch, great care being taken to protect the control plots. The intensity of the fire was low with charred tussock bases remaining after the fire and burnt organic material from the grass and leaf litter remaining on the ground after the fire. No tree foliage was burnt.

Data analysis

Results were analysed using the statistical packages MULTISTAT, SYSTAT version 5 and GLIM. The only higher taxa present in any numbers were Collembola and Acarina which were analysed for samples collected in Oct 1994 (Table 4) and Mar 1995 (Table 5), using the program GLIM with a Poisson error and a logarithmic link. Student's *t* was used to compare taxon abundances between treatments for all sampling dates for which data was sufficient using MULTISTAT and a fully factorial ANOVA using MGLH procedure was conducted for Collembola, Acarina and total invertebrate abundance as dependant variables and the treatment variables, grazing and burning as independant factors for samples from Mar and Sep 1995.

Results

A complete list of taxa collected and numbers in each sample are given in Greenslade and Rowe (1996). The total number of Collembola collected from preburn samples in Nov 1993 was 2434 comprising eight species. Statistical tests (*t*-tests) for significant differences in individuals caught between vertical and horizontal rows of plots showed no biases across the study area. The second pre-burn sample collected only 18 specimens representing four species. These small numbers are almost certainly caused by the lack of rainfall in the preceding months.

Two months after burning numbers were still too low for analysis at species level. However, over three times as many individuals of all groups were collected from the unburnt plots compared with burnt plots and three times as many taxa on the unburnt compared with burnt plots. Similar results were obtained for Collembola alone. Some taxa were only present on the

unburnt plots. Excluding those represented by a single specimen, they were Thysanoptera (24 individuals, 3 species) and Coleoptera (4 individuals, 4 species).

Five months after burning mean numbers of total invertebrates per plot indicated no differences between treatments (Fig. 2). Although only 116 Collembola were trapped, too few for statistical analysis, data for this group did show a slight reduction in numbers on burnt sites both fenced and unfenced, compared with the fenced and unfenced unburnt plots (Fig. 2).

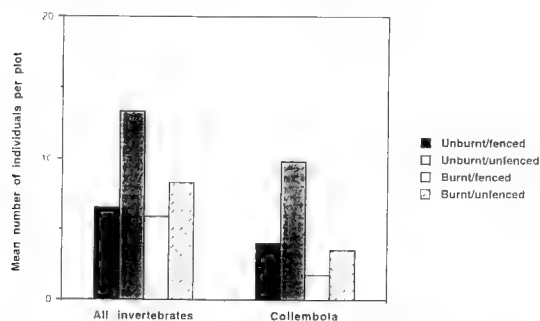


Figure 2. Total invertebrates and Collembola as mean numbers of individuals per plot; five months after burning at Woodstock.

Although total numbers of individuals trapped had increased to over 1000 ten months after burning, numbers of Collembola were still low at 126. However some differences in total numbers between treatments were found to be statistically significant. There was no significant difference between fenced and unfenced control (not burnt) sites. Fenced, burnt plot samples contained twice the number of individuals than the unfenced burnt plots and this difference is statistically significant (t -test, $p < 0.02$) although there was no statistical difference in absolute numbers between fenced burnt plots and control plots (t -test $p < 0.4$) and unfenced burnt plots and control plots (t -test $p < 0.06$) at the level of 5%. Consequently the effect of grazing on total invertebrates at ten months appears to be greater than the effect of fire (Fig. 3A).

Only two species of Collembolan were collected from samples collected ten months after burning, both belonging to the endemic, grass-inhabiting summer active genus, *Coryneophoria*. Eighty-eight percent of one species, *Coryneophoria* sp. 2, individuals were collected on the burnt plots. Alternatively, *Coryneophoria* sp. 1 occurred almost exclusively (95% of individuals) on unburnt controls and burnt fenced plots. Unfenced, burnt sites are intermediate.

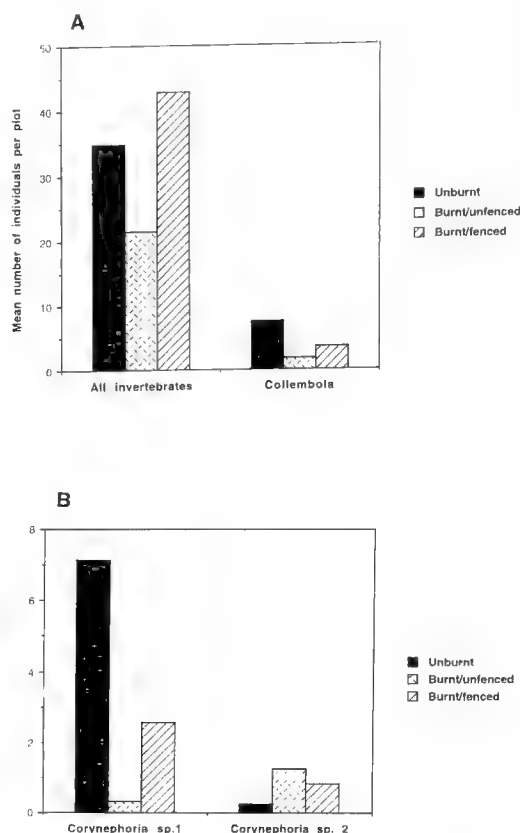


Figure 3. A. Total invertebrates and Collembola as mean numbers of individuals per plot; and B. abundance of 2 collembolan species as mean numbers caught per plot ten months after burning at Woodstock.

At sixteen months the total number of Collembola collected was 2561 but considering control plots alone, this was still only half prefire levels of two years earlier indicating that the some effects of the previous drought were still evident. The winter fauna predominated at this time with no *Coryneophoria* species and Katianninae species being present in large numbers as expected (Greenslade, 1986). There were no statistically significant differences in abundance of total invertebrates between control and treatment or between fenced and unfenced plots. Collembola comprised nearly 70% of total fauna collected. As at ten months, there was no statistically significant difference in total individuals caught between fenced and unfenced control plots (t -test). However there was a highly significant difference between the combined controls and the fenced/burnt plots ($p < 0.001$) and a significant difference between fenced/burnt plots and unfenced/burnt plots ($p < 0.01$). There was less difference between the controls

and the unfenced/burnt plots although this was significant at the 10% level

At the species level further differences were evident in the composition of the collembolan communities. Seventeen species of Collembola were collected 16 months after burning, 12 from unfenced/burnt plots and 14 from fenced/burnt plots. Although the small difference in number of species was not significant, there was a difference in relative species abundance in terms of individuals caught in the two treatments (Fig. 4). The same two species of Collembola were numerically predominant on all treatments but they were relatively more abundant on the fenced plots than on the unfenced plots where the six subsidiary species were more abundant. This is illustrated by the Shannon index of evenness which was 0.356 for the fenced plot and 0.495 for the unfenced plot indicating that the community structure is more evenly distributed among species under grazing.

The comparison "burnt v unburnt" is a comparison between plots, and its mean square

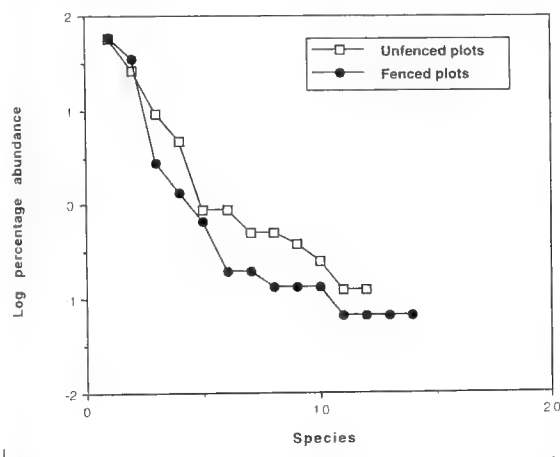


Figure 4. Log percentage species abundance of Collembola caught on fenced and unfenced plots at Woodstock, 16 months after burning.

(m.s.) is therefore compared with the between-plots residual m.s. immediately below it. Similarly, the comparison "grazed v ungrazed" is a within plot comparison, comparable with the within-plots residual. These analyses show no important effects of burning or grazing, except for an effect of grazing on Acarina in 1995, where examination of the data shows that almost invariably there were more Acarines collected on the grazed half plot burnt or unburnt, than on the ungrazed (Table 1). It is not clear whether this is a genuine difference in population density, or merely in sampling efficiency.

Using this analysis based on the Poisson distribution (i.e., random counts), the residual m.s. is expected to equal 1 if there is no heterogeneity. The residual m.s. in the above table show that there is some heterogeneity between plots, but not much within plots. It is therefore not unreasonable to use ordinary χ^2 to examine the effects of grazing (a within plots comparison) on all categories sampled, including those not analysed above, but not effects of burning (a between plots comparison). For example, total Acarines on all ungrazed sub plots in 1995 is 179, on grazed plots is 308; so $\chi^2 = 34.17$ which agrees well with the corresponding m.s. 34.58 in the analysis. Since some within plots heterogeneity does exist, such values of χ^2 should be treated with caution.

Total Collembola, total Acarina and total invertebrates were used as dependant variables in the ANOVA analysis for the two last dates. Several significant values were found as follows. For March 1995, only total Collembola v burning ($p < 0.05$) were significant. In September 1995, for total Collembola both burning ($p < 0.005$) and the interaction of burning and grazing ($p < 0.05$) were significant. Also total invertebrates versus burning ($p < 0.005$) was significant in September 95.

Table 1. Analyses of Deviance obtained from GLIM for October 1994 and March 1995.

	d.f.	October				March			
		Collembola 1994	Acarines 1994	Collembola 1995	Acarines 1995	Collembola 1995	Acarines 1995	Collembola 1995	Acarines 1995
		deviance	m.s.	deviance	m.s.	deviance	m.s.	deviance	m.s.
burnt v unburnt	1	27.09	27.09	0.67	0.67	29.94	29.94	11.79	11.79
between plots residual	14	122.83	8.77	144.91	10.35	86.06	6.15	271.54	19.40
grazed v ungrazed	1	18.76	18.76	1.58	1.58	0.28	0.28	34.58	34.58
withing plots residual	15	49.74	3.32	46.64	3.11	40.92	2.73	15.83	1.06

Discussion

The immediate effect of fire was to reduce invertebrate diversity and numbers of individuals caught, but after eighteen months, both seem to have regained their prefire levels. However, results indicate that the composition of the postfire community is markedly different from that present before burning. This difference is greatest at the level of species as noted by Friend (1996) and is also in agreement with York's results (1994, 1996) from a long term fire study in forest. York found nearly a quarter of ant species were lost from sites which were regularly burnt at three to four year intervals. The evidence here and from York's work strongly suggests that only studies at species level will provide an adequate understanding of the changes caused by burning.

The differences in species composition may reflect differences between taxa in vagility and hence ability to colonise but the proximity of both control and treatment makes this unlikely to be the main reason. Fire changes vegetation structure resulting in a more open plant community with higher day temperatures and low moisture levels at the surface. Measurements of the physical characteristics of the plots were not made but humidity, light and temperature characteristics of the ground surface were probably more important factors determining species composition than vagility.

Closely related species responded in opposite ways to fire in that two *Corynephoria* species differed in their distributions between treatments. The species found most abundantly on burnt plots is widely distributed in Australia while the other species, found more abundantly on controls, is known from other data to be restricted to sites where grass tussocks are well developed and dense.

When the grassy woodland plots were protected against grazing by kangaroos and rabbits, total numbers of invertebrates caught recovered rapidly to prefire levels and at ten months after fire had regained control levels. These results for invertebrates are similar to those found in south-eastern Australia for plants by Leigh and Holgate (1979). In spring, grazing affected the collembolan fauna on the grassy woodland site resulting in a more evenly distribution of individuals between species. At the sampling occasion the interaction between grazing and burning was significant. No difference in species composition was recorded between controls, fenced or unfenced plots but total Collembola

individuals caught increased in fenced plots by increasing numbers of common species caught at the same time as reducing numbers of the subsidiary species. Results from the floristic survey carried out in late 1994 show that the plant cover and hence biomass, was significantly greater on the burnt fenced plots than on burnt unfenced plots and that there were no differences between fenced and unfenced controls (Prober, 1995).

Results must be qualified because of biases caused by the methods used as stressed by Friend (1995). In suction sampling more complex structure and higher density of the vegetation will reduce efficiency of sampling so that the samples from the control plots could be less representative of total populations than those from burnt sites. However a lower number of individuals trapped or caught on the treatment plots, is likely to reflect a real difference in species abundance.

Friend and Williams (1993) studying fire effects on invertebrates in inland heath, found differences between years could be greater than those due to fire. Results here indicated that low rainfall reduced invertebrate numbers for over twelve months to such an extent that data from one preburn sample could not be used, and treatment effects were negligible for five months after burning. In the same experiment Prober (1995) also found that changes in plant species composition were minimal five months after burning and suggested this may have been due to the dry conditions. This indicates that, although obviously desirable (Friend 1995), preburn samples are of value only in detecting variability over the site and can not provide reliable baseline data with which to compare treatment values.

Woodstock cemetery is part of the proposed "Grassy White Box Woodlands Reserve" (Prober, 1995) because of its high conservation value on the basis of floristics and vegetation type. Less than 0.5% of this type of woodland remains in a near-original condition although it once covered several million hectares in the wheat-sheep belt of NSW (Prober and Thiele 1993). As a result of these studies, fire management on this site can take into consideration some of the variable responses of invertebrates to fire and predict the likely consequences of different fire regimes.

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References

- Abbott, I., 1984. Changes in the abundance and activity of certain soil and litter fauna in the jarrah forest of Western Australia after a moderate intensity fire. *Australian Journal of Soil Research* 22: 463–469.
- Abbott, I., Van Heurck, P and Wong, L. 1984. Responses to long-term fire exclusion: physical, chemical and faunal features of litter and soil in a Western Australian forest. *Australian Forestry* 47: 237–242.
- Abensperg-Traun, M. and Milewski, A.V., 1995. Abundance and diversity of termites (Isoptera) in unburnt versus burnt vegetation at the Barrens in Mediterranean Western Australia. *Australian Journal of Ecology* 20: 413–417.
- Andersen, A.N. and Yen, A. L., 1985. Immediate effects of fire on ants in the semi-arid mallee region of north-western victoria. *Australian Journal of Ecology* 10: 25–30.
- Anon, 1992. *An Australian national strategy for the conservation of Australian species and communities threatened with extinction*. Australian National Parks and Wildlife Service: Canberra.
- Cheal, D., 1996. Fire succession in heath-lands and implications for vegetation management. Pp. 67–79 in: *Fire and biodiversity. The effects and effectiveness of fire management. Biodiversity Series, Paper No. 8*. Biodiversity Unit, Department of the Environment, Sport and Territories.
- Cho, G., Georges, A., Stoutjeskijk, R. and Longmore, R., 1995. Jervis Bay. *Kowari* 5. [Australian Nature Conservation Agency Publication: Canberra].
- Coy, R., 1996. The effects of fire on soil invertebrates in *E. regnans* forest at Powelltown, Victoria. Pp. 183–198 in: *Fire and biodiversity. The effects and effectiveness of fire management. Biodiversity Series, Paper No. 8*. Biodiversity Unit, Department of the Environment, Sport and Territories.
- Friend, G.R., 1995. Fire and invertebrates — a review of research methodology and the predictability of post-fire response patterns. *CALM Science Supplement* 4: 165–174.
- Friend, G., 1996. Fire ecology of invertebrates — implications for nature conservation, fire management and future research. Pp. 155–162 in: *Fire and biodiversity. The effects and effectiveness of fire management. Biodiversity Series, Paper No. 8*. Biodiversity Unit, Department of the Environment, Sport and Territories.
- Friend, G.R. and Williams, M.R., 1993. Fire and invertebrate conservation in mallee-heath remnants. *Final report, Project P144, World Wildlife Fund, Australia*.
- Gill, A.M., 1996. How fires affect biodiversity. Pp. 47–55 in: *Fire and biodiversity. The effects and effectiveness of fire management. Biodiversity Series, Paper No. 8*. Biodiversity Unit, Department of the Environment, Sport and Territories.
- Greenslade, P., 1986. Small arthropods. Pp.144–53 in: Wallace, H.R. (ed.), *The ecology of the forests and woodlands of South Australia*. Government Printer: Adelaide.
- Greenslade, P., 1994a. *A study of the use of indicator groups in assessing the conservation value of native grassland sites in the ACT and NSW*. Unpublished report to the ACT Wildlife Unit.
- Greenslade, P., 1994b. Australian native steppe-type landscapes: neglected areas for invertebrate conservation in Australia. Pp. 51–73 in: Gaston, K.J., New, T.R and Samways, M.J. (eds), *Perspectives on insect conservation*. Intercept.
- Greenslade, P. and Rosser, G., 1984. Fire and soil surface insects in the Mt Lofty Ranges, South Australia. *Proceedings of 4th International Conference on Mediterranean Ecosystems. Medecos IV, Perth, August, 1984*.
- Greenslade, P. and New, T.R., 1991. *Australia: conservation of a continental insect fauna*. Pp. 33–70 in: Collins N.M. and Thomas, J.A. (eds), *The conservation of insects and their habitats. Proceedings of the Royal Entomological Society's 15th Symposium 14–15th September 1989*. Academic Press.
- Greenslade, P. and Rowe, I., 1996. *Invertebrate biodiversity in savanna woodlands: does fire enhance species richness?* Unpublished report to Department of Environment, Sport and Territories.
- Greenslade, P., Smith, D. and Floyd, R., 1996. *Short term effects of a fire on invertebrates in coastal heathland on the Beecroft Peninsula: a contribution to the fire management plan for the area*. Unpublished report to the Australian Nature Conservation Agency.
- Hodda, M., 1991. *Ecology of termites in savanna at Kapalga, N.T. Australia*. PhD thesis, Australian National University, Canberra. vii + 224 pp.
- Hutson, B.R. and Kirkby, C.A., 1985. Populations of Collembola and Acarina in litter and soil of South Australian forests and the effects of a wildfire. In: Greenslade, P. and Majer, J.D. (eds), *Soil and litter invertebrates of Australian Mediterranean-type ecosystems. WAIT School of Biology Bulletin* 12: 34–36.
- Little, S.J. and Friend, G.R., 1993. Structure of invertebrate communities in relation to fire history of kwongan vegetation at Tutanning Nature Reserve. *CALM Science* 1: 3–18.
- Lowe, L., 1995. Preliminary investigations of the biology and management of Leichhardt's grasshopper, *Petasida ephippigera* White. *Journal of Orthoptera Research* 4: 219–221.

- Leigh, J.H. and Holgate, M.D., 1979. The responses of the understorey of forests and woodlands of the Southern Tablelands to grazing and burning. *Australian Journal of Ecology* 4: 25–45.
- Majer, J., 1980. Report on a study of invertebrates in relation to the Kojonup Nature Reserve fire management plan. *WAIT Biology Department Bulletin* No. 2.
- Nadolny, C., 1984. *Nature and conservation of the invertebrate fauna in New South Wales rainforests — a preliminary report*. Unpublished report to the NSW National Parks and Wildlife Service.
- Prober, S., 1995. *Establishment and management of the "Grassy White Box Woodlands Reserve" Phase I*. Final report to the Australian Nature Conservation Agency.
- Prober, S.M. and Thiele, K.R., 1993. The ecology and genetics of remnant grassy white box woodlands in relation to their conservation. *Victorian Naturalist* 110: 30–36.
- Tolhurst, K.G., 1996. Effects of fuel reduction burning on flora in a dry sclerophyll forest. Pp. 97–107 in: *Fire and biodiversity. The effects and effectiveness of fire management. Biodiversity Series, Paper No. 8*. Biodiversity Unit. Department of the Environment, Sport and Territories.
- Neumann, F. and Tolhurst, K., 1991. Effects of fuel reduction burning on epigeal arthropods and earthworms in dry sclerophyll eucalypt forest of west central Victoria. *Australian Journal of Ecology* 16: 315–330.
- York, A., 1994. The long-term effects of fire on forest ant communities: management implications for the conservation of biodiversity. *Memoirs of the Queensland Museum* 36(1): 231–239.
- York, A., 1996. Long-term effects of fuel reduction burning on invertebrates in a dry sclerophyll forest. Pp. 163–181 in: *Fire and biodiversity. The effects and effectiveness of fire management. Biodiversity Series, Paper No. 8*. Biodiversity Unit. Department of the Environment, Sport and Territories.

COMPARATIVE ENDEMISM AND RICHNESS OF THE AQUATIC INVERTEBRATE FAUNA IN PEATLANDS AND SHRUBLANDS OF FAR SOUTH-WESTERN AUSTRALIA

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Abstract

Horwitz, P., 1997. Comparative endemism and richness of the aquatic invertebrate fauna in peatlands and shrublands of far south-western Australia. *Memoirs of the Museum of Victoria* 56(2): 313-321.

A study of the peatlands and shrublands in far south-western Australia was undertaken to examine patterns of endemism and richness in aquatic invertebrate faunas. Samples of surface water, interstitial water and crayfish burrow water were analysed from about 45 sites and in each season over a twelve month period in 1993. Six groups of aquatic invertebrates were chosen for more detailed analyses (mites, oligochaetes, isopods, decapods, dipterans, and odonotans) and resolved to species level. For each species an assessment was made of its distributional status as either widespread and common, regionally endemic (to the south-west), or locally restricted to within the study region. Sites with high levels of local endemism were plotted geographically and their characteristics compared to other sites. The data are related to existing hypotheses concerning the depauperate nature of the freshwater fauna of the south-western part of the continent. It was found that such hypotheses need to be tempered by the role of salt in flowing systems, and the occurrence of hot spots of local endemism for freshwater fauna in the extreme south-west in non-flowing waters (and often subterranean habitats) where groups of non-insect invertebrate fauna show apparently elevated species richness.

Introduction

The inland aquatic biota of the south-western corner of Australia has been characterised as being one which displays a relatively high regional endemism, but a conspicuously depauperate richness. For instance the fish and invertebrate faunas of streams are said to be depauperate compared to the freshwater fauna of other temperate regions (Bunn and Davies, 1990). Bunn and Davies based their conclusions on comparisons of family or order level species richness of insects in south-western Australian streams, with those of south-eastern Australia. They proposed that three factors contributed to this reduced richness: the insular nature of the south-west, a previous history of aridity, and an extremely low level of primary productivity, and that these three factors overrode a tendency for higher species richness in areas with a highly predictable climate.

The limnology of the extreme south-west is dominated by an ancient inland plateau which is topographically ill-defined with sluggish water-courses. Closer to the coast there is an area which is still relatively well vegetated, where higher rainfalls produce a steeper topography and more well-defined water courses. In fact the climatic gradients are steep in the far south-

west, with rainfall of 1400 mm per annum near the coast diminishing to 400-500 mm on the inland plateau over 100 km away. Superimposed on these characteristics are trends in the ionic concentrations of the water. Inland in semi-arid areas salt has accumulated in the soil profile from millions of years of aerial deposition. In some places natural salt lakes have formed on old drainage lines. Elsewhere the salt has remained below the ground in the soil profile, and only recently become mobilised by rising water tables resulting from land clearance. All these features combine to give the south-west its unique riverine characteristics, first described by Morrissy (1974) for the Blackwood River. In general, the closer to the coast, the cooler the temperatures, the more rainfall it receives, the steeper the countryside, and the fresher the water. In other words, the river systems in the south-west have reverse longitudinal profiles for temperature, geology, rainfall, topography and salinity.

Despite this conspicuous profile, the macroinvertebrates from the Blackwood River in the south-west display little longitudinality in the fauna composition (Williams et al., 1991). The authors concluded that either the macrofauna might be a good deal more resistant and resilient

to salinity change than currently thought, or the present fauna represents the halotolerant vestiges of a previously more diverse fauna, most of which has been eliminated by rising salinities.

The findings of Williams et al. (1991), along with an understanding of the reverse longitudinal nature of rivers in the south-west, give reason to refine the hypotheses of Bunn and Davies (1990). Given that the latter authors dealt with the insects of flowing waters in their assessment of the depauperate nature of freshwater faunas:

- What role has salt in the landscape played to remove salt intolerant groups of species? Have salt flushes in riverine systems helped to eliminate (over geological time) such faunas? If so, one might expect vestiges of salt-intolerant biota closer to the coast, and possibly in non-flowing waters.
- Accordingly, is the fauna of non-flowing waters also depauperate? Bunn and Davies (1990) make no implication with respect to non-flowing waters. But would an examination of another group of habitats uphold the notions of high endemism and low richness? If aridity was important then faunas that are able to evade aridity by retreating underground with the water should still contain evidence of past richness.
- Does the hypothesis apply to aquatic fauna other than insects? Bunn and Davies examined insect data, then equated these to invertebrates as a whole, as well as to fish.
- Does the hypothesis apply equally to all parts of the south-west? The theory implies that the south-west has been equally affected by aridity and low levels of primary productivity. If the south-west is homogeneous with respect to the effects of primary productivity, insularity and aridity on inland aquatic faunas then there should be no local endemic "hot spots" for aquatic fauna.

This paper aims to examine the above questions, by looking at the invertebrate composition (not just insects) in non-flowing surface and subterranean waters, and in an area which goes from high to relatively low rainfall.

Methods

The study was part of a survey requested by the Australian Heritage Commission to document the heritage values of peatlands and shrublands of the "Southern Forest Region" (SFR) of south-western Australia. The SFR is the administrative region of the Western Australian Depart-

ment of Conservation and Land Management, approximately 170×130 km, which formed the boundary of the study (Figure 1). The region is dominated by karri forests, but many other forest associations and vegetation communities are found within it, including a diverse array of wetland types which occur extensively throughout the region (Wardell-Johnson and Horwitz, 1996 in press).

Forty-five wetland sites were sampled (Figure 1), being chosen if they conformed to one or more of the following characteristics: shrubland vegetation (where there was an impeded drainage), representativeness of geomorphological types (an attempt was made to sample the geographic range of geomorphologically variable wetlands), and wetlands with organically rich soils. In general non-flowing waters were sampled, although at wet times of the year some water flow occurred.

Three habitats types were selected for sampling wherever and whenever they occurred in wetlands: surface water, subterranean water in interstitial spaces (accessed through auger holes) and subterranean water in crayfish burrows.

For surface water habitats, samples were taken by a $125 \mu\text{m}$ mesh sweep net to include littoral emergent and submergent vegetation, benthos and the water column. Subterranean fauna was sampled entirely by siphon, then filtered through a $50 \mu\text{m}$ mesh. All samples were preserved in the field with addition of formalin to make up a solution of 5%. The volume of material collected by these sampling methods prohibited widespread sampling of microhabitats. Physicochemical attributes of water were measured prior to sampling each habitat, and environmental variables including nutrients, basic floristics, soils structure etc. were also taken (Horwitz, 1994).

All samples were washed and filtered through a sieve of mesh pore size of $125 \mu\text{m}$, sorted under the dissecting microscope, specimens removed and stored in 75% alcohol and later identified to species level wherever possible (Horwitz, 1994).

The methods used resulted in an under sampling of freshwater fauna at all scales; regional variability was under sampled because many wetlands were inaccessible or unknown at the time of choosing sites; local habitat variability was under sampled because some wetlands had a diversity of wetland types (ie. swamp, pool, creek, lake), which were not all sampled; and microhabitat variability was under sampled because only one sample was taken for each type

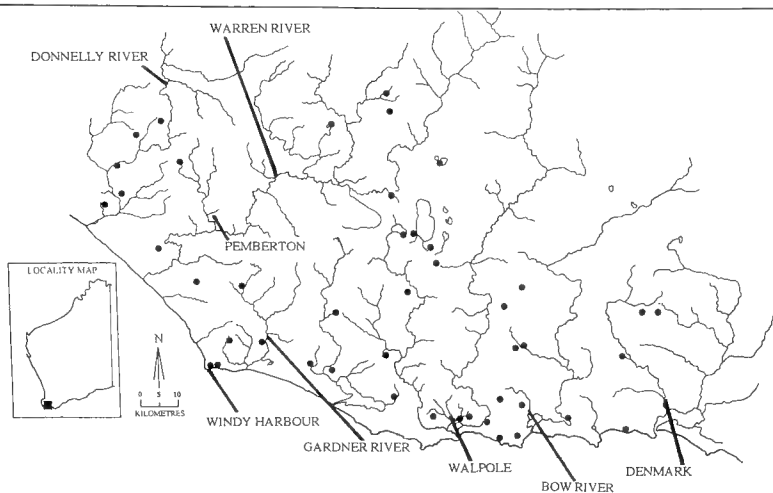


Figure 1. Map showing the approximate extent of the Southern Forest Region of extreme south-western Australia, with wetland sites sampled in this study, and locations of place names used in the text.

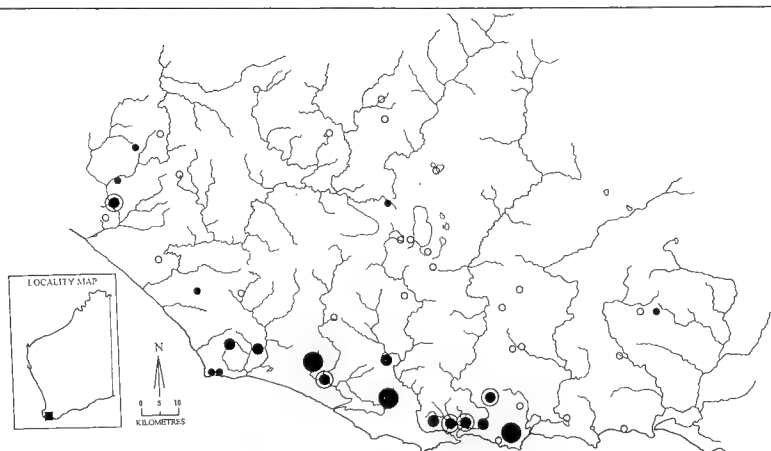


Figure 2. Map of the study area showing sites with a relatively high proportion of locally restricted species, where small dot = 1–5%, medium dot = 5–10%, medium dot ringed = 10–15%, and large dot = >15%.

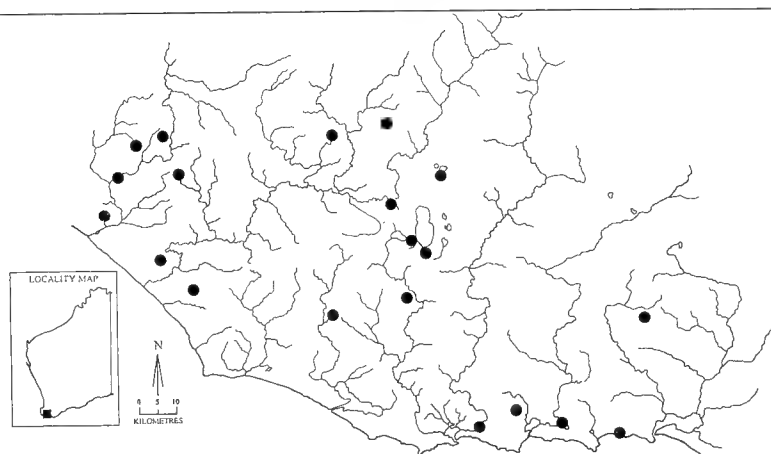


Figure 3. Study sites showing sites (solid circle) with greater than 20% of their aquatic invertebrate fauna which could be classified as common and widespread.

at each visit where possible (replicated sampling showed that one sample might result in somewhere between 40–70% of fauna present at that time (see Horwitz 1994)). In addition, the sampling methods were designed to capture very small animals since these were identified as potentially interstitial; therefore the methods selected for slower swimming fauna because the fine meshed nets clogged very quickly and faster swimming species could escape. For these reasons it can be assumed that the methods resulted in an underestimation of the local fauna at a site, so that an absence of a taxon at a site may not be real. Nevertheless, these limitations are common in regional surveys of this type, and such methods should be sufficient to indicate patterns in the relevant biota.

The faunal suite collected included all the known freshwater forms expected in a study of this sort, but in order to reduce the data set to a manageable form, several taxonomic groups were examined in detail to represent the fauna as a whole:

- a highly vagile group (Odonata);
- a group that is dominant in terms of biomass, with both vagile and restricted elements (Decapoda);
- the most diverse group (Diptera, in particular the Chironomidae);
- a group likely to contain taxa which show restricted distributions (Isopoda);
- a group whose larval stage is parasitic on other elements of the aquatic fauna (Acarina); and
- a group mostly wedded to the benthos (Oligochaeta).

With the assistance of taxonomic experts each species or taxon was categorised as belonging to one of the following status groups (where possible):

- Common — species or species groups which are known to occur across southern Australia (in both SW and SE Australia) and/or species which are known to occur outside the south-western Australia.
- Regional endemics — species proposed to be endemic to south-western Australia, either distributed throughout the south-west, or more restricted in distribution but not found exclusively within the study area
- Local endemics — species which are hypothesised to occur only within the study area. Taxa in this category are subject to the limitations given above.

Results

Table 1 shows the richness of each group and the number of taxa which could be apportioned to one of the three categories. Notes on the occurrence of taxa in each major group are given below; more details are available in Horwitz (1994).

Oligochaeta

Twenty three taxa belonging to five families were represented in the freshwater worm collections (Table 1). Enchytraeid worms were found at about two-thirds of the sites, but were unresolved beyond the family level. The Capilloventridae is monogeneric but the other three freshwater congeners are restricted to south-eastern Australia (Pinder and Brinkhurst, 1994), so this represents the first find in the western part of the continent. It was found in sandy sediments of low shrublands. Eight phreodrilid species were found in the collections, none of them previously known from Western Australia. The phreodrilid fauna included two common and widespread species (*Insulodrilus nudus* and *I. lacustris*). Two species, *Insulodrilus* sp., and *Antarctodrilus* sp., occurred across the study region. Two further undescribed phreodrilids were relatively rare in the collections, being found only close to the coast between Gardner River and Walpole, and two more undescribed species (including an *Antarctodrilus* sp.) have similar distributions to the latter species but with one or more distributional outliers. Three distinctive species in the family Tubificidae were found (each from only one site), along with two forms of immature tubificid taxa. A new species in the genus *Ainodrilus* is the second freshwater species of this small genus, the other is known only from billabongs in the Northern Territory (Pinder and Brinkhurst, 1994). *Limnodrilus hoffmeisteri* is a very common species (and also known from one site in the Perth region; A. Pinder, pers. comm.), and was found once in the study area. *Telmatodrilus* ?sp. is morphologically similar to a Tasmanian species, and was found at only one site in interstitial water. In the family Naididae, three forms of the cosmopolitan genus *Pristinella* were recognisable, two of them relatively widespread, and one found at one site only. Five (otherwise geographically widespread; Pinder and Brinkhurst 1994) species were also recorded: *Pristina longiseta* from across the study area, *P. aequiseta* from one site only, *Dero furcatus* from four sites across the study region,

Table 1. Six groups of aquatic invertebrates which were examined in detail, showing the total number of taxa in each family. Where possible, each taxon was given a status category (see text; Common = common and widespread taxon, known to occur elsewhere in Australia, Regional E = taxon known to be endemic to the south-west but not restricted to the study area, Local E = taxon thought to be restricted to the study area). In most cases there were taxa which could not be assigned to one or other of the categories. For more details see text.

		Total No. Taxa	STATUS OF SPECIES		
			Common	Regional E	Local E
Oligochaeta	Capilloventridae	1			1
	Phreodrilidae	8	2	3	3
	Tubificidae	5		2	
	Naididae	8	5		
	Enchytraeidae	?			
	Total No.	23	7	5	4
Acarina	Arrenuridae	2	1	1	
	Aturidae	2		2	
	Eylaidae	1	1		
	Halacaridae	?	?		
	Hydrachnidae	1	1		
	Hydrodomidae	1	1		
	Hydryphantidae	2	1		1
	Hygrobatidae	2	1	1	
	Limnesiidae	1		1	
	Limnocharidae	1	1		
	Mideopsidae	1		1	
	Momoniidae	1		1	
	Oxidae	2	1	1	
	Pezidae	2		1	1
	Unionicolidae	3	3		
	Total No.	23	11	9	2
Isopoda	Janiridae	(2)		(1)	(1)
	Phreatoicoidea	?		?	?
Decapoda	Parastacidae	7		5	2
	Palaemonidae	1		1	
	Grapsidae	1	1		
	Total No.	9	1	6	2
Diptera	Orthocladiinae	24	8	2	1
	Chironominae	29	18	4	
	Tanypodinae	8	4	3	
	Aphroteniinae	2	2		
	Total No.	63	32	9	1
Odonata	Coenagrionidae	2	1		
	Megapodagrionidae	2		1	
	Lestidae	3	2		
	Gomphidae	1		1	
	Aeshnidae	3	1	1	
	Cordulidae	6	1	2	
	Libellulidae	5	3	1	
	Total No.	22	8	6	
Totals		142	59	36	11

and *Dero digitata* from three sites with permanent water, and these species have also been found in wetlands on the Swan Coastal Plain. The fifth, *Chaetogaster diastrophus*, a globally widespread predatory worm, was previously known only from LaTrobe River in Australia, and found at one site. The most species rich site in the study contained 10 oligochaete taxa. The capilloventrid, and three of the undescribed phreodrilids were hypothesised to be restricted to the study area.

Acarina

The acarine fauna collected in the study area represented four suborders; of these only the known aquatic forms from the suborder Prostigmata were resolved taxonomically to genus or species. Twenty-three taxa were recorded, including:

- those endemic to south-western Australia: two new species in the family Pezidae (one of which is a new genus); *Wheenyoides cooki* (previously only known from two other locations); *Pseudohydryphantes doegi* found from one site, previously thought to have been extinct; and *Arrenurus* sp. near *tasmanicus* which is endemic but widespread in the south-west. Of these the new pezid genus, and *Pseudohydryphantes*, were regarded as locally restricted endemics.
- species in Gondwanan genera which are almost certainly endemic and restricted in their distributions, but not necessarily to within the study region (*Corticacarus*, *Axonopsella*, *Momoniella*, *Gretacarus*).
- species widespread in southern Australia (*Limnochares australica*) or species in a widespread genus in Australia (*Coaustaliobates*).
- species in cosmopolitan genera (*Hydrachna*, *Eylais*, *Hydrodroma*, *Diplodontus*, *Oxus*, *Fron-tipoda*, *Unionicola*, *Koenikea*, *Arrenurus*).

The most common taxon found in the collection was the halacarid mite, forms of which have also been found in cave material and on the Swan Coastal Plain (M. Harvey, pers. comm.). The richest site for water mites contained 11 of the 24 taxa.

Isopoda

Three main types of isopod were collected. Those belonging to the Oniscoidea are traditionally thought to be terrestrial rather than aquatic, but are regular components in some aquatic situations. Oniscoids collected in this study which came from crayfish burrows or auger holes are likely to have been fall-ins, but those from surface waters may be truly aquatic.

Phreatoicoidea were collected from wetland sites close to the coast between Bow Bridge and the Donnelly River, belonging to endemic species in the genus *Amphisopus*. Four taxa were found, including one described species (*A. annectens*) and three undescribed morphological forms (which may all be separate species, B. Knott pers. comm.). One of the forms was restricted to interstitial or crayfish burrow habitats in the Windy Harbour/Walpole region. For the purposes of determining their distribution status, *A. annectens* was deemed regionally endemic since it also occurred outside the study area, and the undescribed forms were collectively (and conservatively) considered to be one taxon which occurred only within the study area (ie. locally endemic).

Janirid isopods had not previously been recorded from south of Yanchep caves near Perth, although being widespread in south-eastern Australia. They were collected from 12 sites between Bow Bridge and Donnelly River in mainly coastal locations where their occurrence is thought to be associated with burrows of the crayfish genus *Engaewa* (at 11 out of 12 sites). A preliminary investigation of janirid isozyme electrophoresis using two populations in the study area, and two from outside the study area (one near Margaret River, and one near Yanchep), revealed that all four populations displayed large amounts of fixed isozymic differences in allopatry. A similar situation has been found in south-eastern Australia for these crustaceans (Horwitz, Andrew and Knott, unpubl.). Thus, two genotypes are recognised in this study, one from western sites near the Donnelly River; this taxon is deemed regionally endemic since it is likely to be found west (outside) of the study area (albeit still restricted). The second is regarded as locally endemic, and is located centrally.

Decapoda

The freshwater decapod fauna is represented by shrimps, crabs and crayfish. The shrimp "*Palaemonetes australis*" was collected from both coastal and inland sites with surface water. It is a widespread endemic species in the south-west. The crab *Leptograpsodes octodentatus* occurs in fresh or brackish areas on the southern coastline of Australia, particularly at contact zones between limestone and granite where freshwater seepages are established. Freshwater crayfish include the genera *Cherax* and *Engaewa*. Four species of the Australia-wide genus *Cherax* were collected: *C. tenuimanus*

(marron) from two permanent water sites, *C. preissii* (koonac) from most sites, and *C. quinquecarinatus* (gilgie) from eight sites. The fourth species, *C. crassimanus* is more restricted to the extreme south-western corner of the state, and was located at seven sites, principally those with organic rich soils. These species are all regional endemics.

The genus *Engaewa* is also restricted to the extreme south-western part of Australia. Three species were found in this study: *E. similis* was found in the western part of the region, around the Donnelly River; *E. subcoerulea* occurred at 8 sites between Gardner River and Bow River; and an undescribed species was located from two sites between Walpole and Bow River. The latter two species can be regarded as being locally endemic.

Diptera

One hundred and fifteen dipteran taxa were collected and identified, representing 12 commonly occurring families. Sixty three chironomid taxa were found. In distributional terms the taxa tended to fall into one of three groups:

- taxa generally widespread and common in the study region and beyond, including for instance *Limnophyes pullulus*, *Chironomus* aff. *alternans*, *Cladopelma curtivalva*, *Dicrotendipes* sp. V47, *Tanytarsus* sp., *Procladius paludicola*, *Paramerina levidensis*, *Alotanytus dalyupensis*, *Tanypodinae* ?gen.?sp., *Pentaneurini* Genus C (previously only known from northeastern Tasmania);
- rare taxa from one, two or three sites, including: ?*Limnophyes* sp.; *Stictocladius* spp. V35 and near V70, *Orthocladinae* spp. VND1 and V15, *Cladopelma* sp., *Dicrotendipes* ?*conjunctus*, *Paratanytarsus grimmi*, *Polypedilum* nr. V33, *Stenochironomus* V27, *Aspictrotanytus* V9, *Aphroteniella tenuicornis*; some of these taxa are common and widespread (like *P. grimmi*), while one could be regarded as truly rare and restricted, and Gondwanan in origin (*Stictocladius* sp. near V70) (Edward, pers. comm.); and
- taxa with disjunct, generally coastal distributions; for instance *Paratendipes* V12, *Polypedilum* spp. V3, near V3, and V33, *Riethia* spp. V4 and V5, and *Stempellina* ?*australensis*.

Several of the taxa mentioned in the first two groups are common elements of the chironomid fauna found in eutrophic wetlands on the Swan Coastal plain (see Pinder et al., 1991).

Odonata

Twenty two taxa, including seven unidentifiable immature odonates, representing seven families and one subfamily, were collected. The most frequently collected species were *Austrolestes analis* (13 sites) and *Orthetrum caledonicum* (eight sites); most other taxa were collected at five sites or less. Odonate rich sites were invariably permanent water sites where sampling occurred amongst emergent or submergent vegetation. Synthemistinae were rarely found in crayfish burrows. No locally restricted taxa, and only five regionally endemic species were found (*Argiolestes minimus*, *Austrogomphus* ?*collaris*, *Austroaeschna anacantha*, *Procordulia affinis*, and *Synthemis cyanitincta*).

Discussion

Endemism, freshwater fauna and salinity

The category of locally endemic should be taken as an hypothesis which can be tested by detailed surveys for distributional points in subsequent studies, but should also serve as a focus for the regional importance of, and immediate conservation value of, freshwater fauna in the far southern wetlands. As described above, eleven taxa were regarded as being included in this category. It is therefore plausible to assume that approximately 8% at least of the freshwater fauna in the southern wetlands are locally restricted in distribution, and high in conservation value. These local endemics were not shared equally across all groups. Highly vagile groups of taxa (Odonata and Diptera) demonstrated low levels of local endemism, and groups with a perceived low vagility, which were apparently wedded to sandy, or organic-rich, saturated soils (ie. Oligochaeta, Isopoda and Decapoda) contained taxa which were hypothesised to be restricted in their distributions.

By geographically plotting the proportion of locally restricted taxa at any one site, Figure 2 shows that the highest proportions are found in the central, more coastal, sites of the study area. Inland, the potential for such species to occur still exists although less frequently in the data set. A high proportion of common species occur more at inland sites (Figure 3).

Although environmental predictors for the occurrence of endemic or common species are yet to be fully determined, it would appear that a site proximal to the coast, in the Walpole — Windy Harbour part of the study area is likely to harbour locally restricted endemics if those species exhibit an interstitial mode of existence.

This area corresponds to the highest rainfall part of the study region, and of the south-west in general. Wetlands here are influenced by all year round rainfall, with less seasonal water levels fluctuating near the surface in peatlands and shrublands, where such wetlands are frequently dystrophic. Fauna which require freshwater are more likely to be found in habitats which allow contraction to sediments to avoid less frequent and unpredictable aridity.

Further inland rainfall decreases, its seasonality increases, and the occurrence of saline wetlands increases. Indeed, the proportion of common species found at a site is significantly positively correlated with the (log of the) salinity of the surface water ($n=41$, $r=0.315$, $p<0.05$). These observations suggest that species which are common and widespread in the south-west are also those which are more likely to be able to tolerate seasonal rainfall and seasonal aridity, and saline waters of varying concentrations. Fauna requiring waters with a low ionic concentration of salts are unlikely to be found in inland wetland sites unless they are highly mobile and have other life history characteristics which enable them to capitalise on the sporadic occurrence of surface fresh waters.

Comparative richness

Seeking comparative information about the richness of groups in different areas is always fraught with methodological and taxonomic complications. An objective comparison can only be made where similar methods (particularly mesh size of nets), similar effort (with respect to seasonal sampling and habitats chosen), over a similar area with as many sites, are used. Taxonomic effort for each group must also equate. Realistically this is almost impossible to achieve. Perhaps the biggest obstacle for this study has been the absence of a similar-sized regional survey of these habitats from elsewhere in Australia, and the only recent emergence of a sound taxonomic basis for groups such as decapods, isopods, oligochaetes and acarines. Nevertheless, some comparisons are instructive.

For instance studies of the freshwater macroinvertebrate fauna of dune lakes of south-eastern Queensland and north-eastern New South Wales by Bayly et al. (1975), Bensink and Burton (1975), Arthington and Watson (1982) and Arthington et al. (1986) recorded only two oligochaete, six acarine, four decapod and no isopod species, yet 50 odonate species. Similarly, Timms' (1985) summary of species richness in the macrobenthic communities of a few

maars and acid lakes in south-eastern Australia records low numbers of oligochaete and acarine species. The records of nine decapod species, 23 oligochaete and 23 acarine taxa in this survey from a temperate region of this size, cannot necessarily be regarded as "depauperate" for those taxa.

Conclusion

These data and speculations allow a refinement of the hypotheses of Bunn and Davies (1990), assuming that the component missing from the "depauperate" south-west is that which requires fresh water. Thus, periods of aridity and salinisation have contributed to a demise of taxa which live in waters with low ionic concentrations. Freshwater fauna in flowing waters will be vulnerable to extinction due to periodic flushes of saline waters from inland parts of catchments, increasing seasonality of rainfall and periodic aridity. Freshwater faunas of non-flowing waters have been forced to contract towards the coast where rainfall is less seasonal, where waters are more dystrophic, and where an interstitial habitat has been reliably available. In these areas, an endemism "hot spot", and indeed an apparently high richness in some non-insect groups, has been retained.

These notions are supported in part by the conclusions of Storey et al. (1993), who suggested that rotifers and microcrustaceans, with their drought resistant stages and poor dispersal characteristics, show high endemism and considerable radiation in coastal south-western Australian lakes, and that these coastal habitats probably provided refugia during arid periods.

In an unpublished report Main and Main (unpubl.) assessed and mapped the occurrence of fauna with Gondwanan affinity and therefore relictual status in south-western Australia. They argued that Gondwanan elements were likely to be found in, among others, high rainfall areas with short summer drought, areas adjacent to granite rocks from which water is shed, areas of impeded ground water flow so producing winter wet swamps, areas with southern or south-western aspect (thus sheltered from summer insolation), and sites with deep organic litter which gains moisture. While no evidence is presented here to demonstrate that the invertebrate species which characterise the southern "hot spot" are of Gondwanan origin, the concordance between the high levels of endemism, the dystrophic moist habitats, and the predictions of Main and Main, warrant both further research, and cau-

tious management activities which avoid enhancing seasonal aridity in the far south-west.

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References

- Arthington, A.H. and Watson, J.A.L., 1982. Dragonflies (Odonata) of coastal sand-dune fresh waters of south-east Queensland and north-east New South Wales. *Australian Journal of Marine and Freshwater Research* 33: 77-88.
- Arthington, A.H., Burton, H., Williams, R.J. and Outridge, P.J., 1986. The ecology of humic and non-humic dune lakes, Fraser Island, with emphasis on sand infilling in Lake Wabby. *Australian Journal of Marine and Freshwater Research* 37: 743-764.
- Bayly, I.A.E., Ebsworth, E.P. and Hang Fong Wan, 1975. Studies on the lakes of Fraser Island, Queensland. *Australian Journal of Marine and Freshwater Research* 26: 1-13.
- Bensink, A.H.A. and Burton, H.B., 1975. North Stradbroke Island — a place for freshwater invertebrates. *Proceedings of the Royal Society of Queensland* 86: 29-45.
- Bunn, S. and Davies, P., 1990. Why is the stream fauna of south-western Australia so impoverished? *Hydrobiologia* 194: 169-176.
- Horwitz, P., 1994. *Patterns of endemism in the freshwater fauna of the far southern peatlands and shrublands of south-western Australia*. Report to the Australian Heritage Commission and Heritage Council of Western Australia. 43 pp.
- Main, A.R. and Main, B.Y. (unpubl.). *Report on the Southern Forest Region of Western Australia*. Unpublished Report to the Australian Heritage Commission.
- Morrissy, N.M., 1974. Reversed longitudinal salinity profile of a major river in the south-west of Western Australia. *Australian Journal of Marine and Freshwater Research* 25: 327-335.
- Pinder, A.M. and Brinkhurst, R.O., 1994. A preliminary guide to the identification of microdile Oligochaeta of Australian inland waters. *Identification guide No. 1, Cooperative Research Centre for Freshwater Ecology*.
- Pinder, A., Traylor, K.M. and Davis, J.A., 1991. *Chironomid control in Perth Wetlands. Final Report and Recommendations Prepared for the Midge Steering Committee*. Murdoch University, Western Australia.
- Storey, A.W., Halse, S.A. and Shiel, R.J., 1993. Aquatic invertebrate fauna of the Two Peoples Bay area, southwestern Australia. *Journal of the Royal Society of Western Australia* 76: 25-32.
- Timms, B.V., 1985. The structure of macrobenthic communities of Australian lakes. *Proceedings of the Ecological Society of Australia* 14: 51-60.
- Wardell-Johnson, G. and Horwitz, P. (in press). Conserving biodiversity in ancient heterogeneous landscapes: a case study from south-western Australia. *Forest Ecology and Management*.
- Williams, W.D., Taaffe, R.G. and Boulton, A.J., 1991. Longitudinal distribution of macroinvertebrates in two rivers subject to salinization. *Hydrobiologia* 210: 151-160.

THE USE OF PITFALL TRAPS FOR SAMPLING ANTS — A CRITIQUE

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Abstract

Majer, J.D., 1997. The use of pitfall traps for sampling ants — a critique. *Memoirs of the Museum of Victoria* 56(2): 323-329.

Invertebrates, especially ants, are increasingly being used in terrestrial surveys and the most commonly used sampling method is pitfall trapping. Pitfall traps may not be effective for species associated with soil, deep litter and vegetation. By drawing on the author's data on ants in a range of ecosystems of increasing complexity, catches obtained by pitfall traps are compared with those obtained by a complementary suite of sampling procedures. The findings indicate that pitfall traps alone undersample the complete ant community and provide a skewed representation of the ant functional groups. The outcome of this analysis of existing data is that a full sampling protocol, which adequately samples ants and other terrestrial invertebrates, should be used when censusing communities.

Introduction

Now that invertebrates are an accepted part of the conservation agenda, an increasing number of surveys of terrestrial invertebrates are being carried out. Topics for which invertebrates have recently been assessed include the impact of forestry practices (York, 1994), the success of mine-site rehabilitation (Andersen, 1993), the comparison of different agricultural management tools (Greenslade and Smith, 1994), the impact of disturbance in conservation areas (Burbidge et al., 1992) and the assessment of biological diversity within regions (Yen et al., 1989).

One group which has received considerable attention in Australia is the ants, so much so that guidelines have been drawn up for their use as bioindicators of the condition of the environment (Majer, 1983; Andersen, 1990). The utility of this taxon is such, that scientists and consultants use it as a bioindicator taxon in all states and territories of Australia. Examples of the use of ants as indicators and in biological surveys have been documented in Beattie (1993).

The most commonly used method for sampling ants in Australia is pitfall trapping and some studies have relied solely on material obtained by this procedure (e.g., Majer, 1977; Yeatman and Greenslade, 1980; Andersen and Yen, 1985; York, 1994). This is reasonable if the study is specifically investigating surface-active ants, but there is a tendency to use this as a surrogate for the entire ant community of the habitat. The ants are generally sorted to species level and analysed in terms of relative abundance of species, species richness, functional group profile and then, using multivariate techniques such

as ordination and classification, in terms of species composition.

Pitfall traps have been adopted because they are relatively simple to use, they operate continuously through day and night over extended periods, and they yield high numbers of ants representing a range of species. However, the procedure used affects the results from pitfalls in a variety of ways (Adis, 1979; Luff, 1975). For example, Abensperg-Traun and Steven (1995) evaluated the influence of trap diameter on the number of species caught in eucalypt woodland and found that size affected results. They also found that the number of species caught continued to accumulate up until at least 16 traps. Marsh (1984) found that pitfall trapping did not provide an accurate representation of the epigeic ant community in the Namib desert and suggested that this was caused by differences in the susceptibility of some species to being trapped. In Venezuela, Romero and Jaffe (1989) compared pitfall trap catches with bait samples and hand collections taken from defined areas or over standardised time periods. Although pitfall trapping was found to be an efficient procedure, it did not collect the full range of species which were present, thus leading the authors to conclude that it should be combined with hand collecting if a more complete community census is required. Andersen (1991) compared catches from pitfall traps with those collected by hand from small quadrats in Australian savannah. He concluded that both procedures provided a similar representation of the epigeic ant community, although he suggested that pitfall traps might provide an inadequate census in less open

habitats where litter impedes surface activity and cryptic species are more important.

The above-mentioned critiques have each addressed specific questions about the efficacy of pitfall trapping. This paper looks at the performance of pitfall traps against a more complete suite of techniques for censusing the entire ant community in habitats of increasing complexity. Three studies of minesite rehabilitation are used for this evaluation as they represent a gradation in habitat complexity from eucalypt forest in North Stradbroke Island, Queensland to dune forest at Richards Bay, South Africa, through to tropical rain forest at Trombetas, Brazil. Within each study, the succession from the newest rehabilitation through to the original vegetation also represents a trend of increasing habitat complexity. Secondly, unpublished data from a Western Australian forest are used to evaluate the efficacy of repeated pitfall trapping at one site as a means of censusing the ant community. It should be noted that the individual studies reported on here were originally self-contained projects; hence differences exist between the exact method and equipment used.

Study sites

At all three minesites a range of rehabilitated plots, ranging from very recent through to the oldest examples, and three controls, representing the pre-mining situation, were selected.

The North Stradbroke Island study was of a mineral sand mine. Twelve areas of rehabilitation, ranging from 0.1 to 15 years, were studied and the controls consisted of two open forest and one high closed scrub plot. A full description of the plots appears in Majer (1985).

The Richards Bay study was also of a mineral sand mine. Here eight rehabilitated plots, ranging from 0.3 to 13 years, and three pre-mining controls of dune forest were studied. Full details of the plots are given in Majer and de Kock (1992).

The Trombetas study was of a bauxite mine in the Brazilian Amazon. It included nine rehabilitated plots, ranging from 0.3 to 11 years, and three pre-mining rain forest plots. One of the control plots was an annually inundated plot (C₃) where ant species richness was lower than upland forest (Majer and Delabie, 1994). Full details of the plots are given in Majer (1995).

Although this was never actually quantified in a manner where comparisons could be directly made, it should be emphasised that the veg-

etation in the control plots of the Australian, South African and Brazilian rehabilitation studies represents a trend of increasing structural complexity (see data in original publications). Secondly, the succession from recent rehabilitation to the oldest examples within all three localities also represents a gradient of increasing complexity (see data in primary references). Finally, the rehabilitation attains a complex structure more rapidly in the Brazilian and, to a lesser extent in the South African, mines which were studied.

The Western Australian forest site was situated near Dwellingup, where it formed the control plot for the ongoing study of ant succession in rehabilitated bauxite mines (Majer, 1981).

Ant survey procedures

Similar, but not identical, sampling procedures were utilised in the minesite succession studies. First a 100 m transect was marked out in the centre of each plot and ant collecting was performed along, and within 20 m of this line.

Ten pitfall traps (43, 25 and 20 mm internal diameter at North Stradbroke, Richards Bay and Trombetas respectively) containing ethanol/glycerol preservative were established at equal distances along the transect and run for 7 days. Day collections were performed for two person hours per transect and consisted of visual searching of soil, litter and vegetation as well as sweeping of undergrowth and beating of trees. At Trombetas, sweeping and beating were each carried out for 2 person hours so day collecting was more intensive than at the other two sites. Night collecting was carried out by visual searching for 1–1.5 person hours. Litter was collected from along the transects of all plots at North Stradbroke, the 13-year old rehabilitation and one control at Richards Bay and from the 5- and 11- year old rehabilitation and all controls at Trombetas. Litter ants were extracted by Tullgren funnels at North Stradbroke and Richards Bay and by Winkler sacks at Trombetas. Finally, at Richards Bay and Trombetas, the surface-active ants were respectively sampled by fish/honey and fish/honey/biscuit baits. Baiting was only carried out on those plots where litter samples were taken. The plots sampled by pitfall trapping plus day and night collecting were censused by what I refer to as the 'standard' sampling regime, whereas those also sampled by litter extraction or by litter extraction plus baiting were censused by the 'extended' sampling regime.

The Western Australian forest site was sampled by a grid of 6 x 6 18 mm internal diameter pitfall traps spaced at 3 m intervals. Traps were run monthly for 7 day periods from March 1976 to December 1977.

In all four studies ants were sorted to species level and assigned species code numbers within each genus.

Results and discussion

The full results of these studies are described in the references listed above. Here I concentrate on the efficacy of pitfall trapping in providing a census of the ant species present within these areas.

Figures 1a, b, and c show the numbers of ant species caught per plot by pitfall trapping and the additional number of species caught by day collecting, night collecting, litter sampling and baiting. Note that, with the exception of litter sampling at North Stradbroke, litter sampling and baiting were only performed in selected plots. Thus, the combination of pitfall trapping plus day and night collecting is generally the measure of species richness that may be universally compared between plots.

The pattern of build up in the ant fauna was not linear at any of the sites. At North Stradbroke and Richards Bay ant richness built up and then declined for a period when *Pheidole megacephala* reached high densities (Majer, 1985; Majer and de Kock, 1992), before increasing once again. Species richness peaked at around 5 years at Trombetas and exhibited some oscillations thereafter (Majer, 1995).

The pitfall trap catch showed broadly similar trends to those shown by pitfall trapping plus day and night collecting, although the number of species trapped was considerably less than the cumulative richness. Furthermore, although the number of species in pitfall traps was correlated with the number of species obtained by the standard sampling regime at all three sites, the percentage variance explained declined with increasing habitat complexity (73%, 59% and 47% at North Stradbroke, Richards Bay and Trombetas respectively). Thus the ability for the pitfall trap catch to act as a surrogate for overall species richness lessens as the complexity of the habitat increases.

Table 1 shows the mean number of ant species caught by pitfall trapping expressed as a percentage of those caught by the standard and extended samples in rehabilitation and native vegetation at the three localities. A number of trends are clearly evident.

Firstly, pitfall trapping never obtained more than 60 % of the ant species obtained from the more complete sample sets. Secondly, looking at the standard sampling set data first, the percentage of ants trapped by pitfall trapping in the control plots was always considerably lower than in the rehabilitated plots. Thus, pitfall trapping does not sample a constant proportion of the fauna if widely divergent habitats are considered. Thirdly, the shortfall in pitfall trap catch increased in both rehabilitation and controls with the increasing habitat complexity

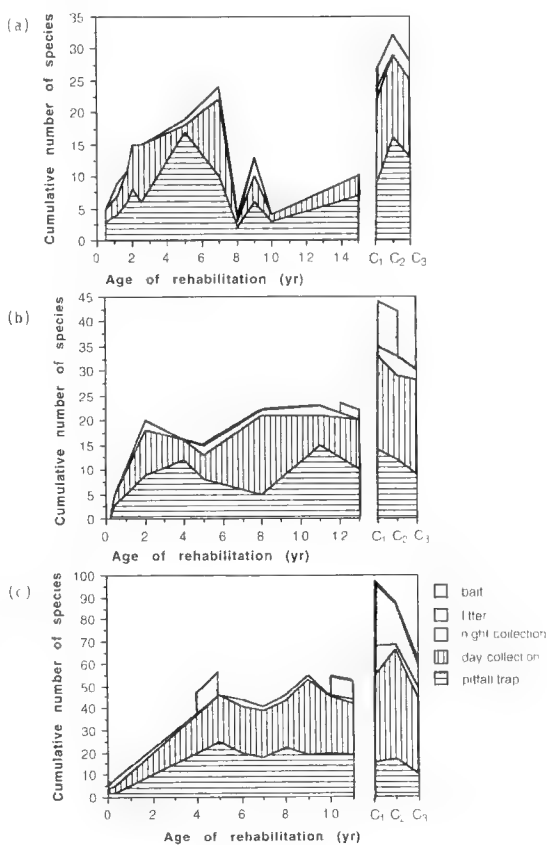


Figure 1. Number of ant species caught in rehabilitated and native vegetated control plots (C1–3) by pitfall trapping and with the addition of day collecting, night collecting, litter sampling and baiting. Data are for (a) North Stradbroke Island, Australia, (b) Richards Bay, South Africa and (c) Trombetas, Brazil. Note that baiting was not performed at North Stradbroke and baiting plus litter sampling were only performed in selected plots at Richards Bay and Trombetas.

from North Stradbroke, through Richards Bay to Trombetas. In the forest at Trombetas the pitfall traps only sampled an average of 22.3 % of the species obtained by the standard sampling regime.

If the data from the extended sampling regime are used for the calculation of percentage catch by pitfall traps, the trends are further exaggerated (Table 1), although direct comparison of the standard and extended sample percentages is complicated by the fact that the extended sample averages are only calculated from a subset of plots.

Which ants are not sampled by the pitfall traps? Inspection of the species lists indicates that cryptic, hypogaecic ants and arboreal nesting species are the groups which are most likely to be undersampled. The increasing tendency for arboreal nesting and the increased litter layer in the more tropical environments in part accounts for the decreased efficiency of pitfall traps. A further category which is undersampled is the rare ants; those which are only likely to be sampled occasionally as a result of their sparse distribution and/or low numbers (Abensperg-Traun and Steven, 1995). Although there is a high chance of missing them in the row of pitfall traps, a diligent search over a less restricted area tends to reveal them.

The conclusion from this comparative analysis is that pitfall trapping provides an inadequate census of the ant community of an area and this problem becomes more pronounced as the structural complexity of the habitat increases.

A procedure which is commonly used when conducting ant surveys is the examination of the functional group profile of the fauna. This is a procedure which was originally developed by

Greenslade and Thompson (1981) and refined by Andersen (e.g., 1990). How useful is this procedure, if the full community has not been sampled? This can only be investigated at North Stradbroke Island, since the scheme was specifically designed for Australian ants.

Figure 2 shows the functional group profiles for the rehabilitated and forest control plots at North Stradbroke Island. The data have been expressed as percentages of the total ants caught by each sampling regime in order to make the two graphs visually comparable. It is immediately obvious that the pitfall traps generally sampled ants from a smaller number of functional groups than did the standard sampling regime. Also, the proportions of species in the various functional groups tends to deviate considerably between the two sets of data. Thus, any study which categorises ants into functional groups on the basis of pitfall trap data alone is in danger of producing findings which differ from those which would be obtained by a more complete census of the fauna.

The data presented here indicate that there are severe limitations in relying on pitfall trap data alone for censusing ant communities although, in part, the efficacy of the traps may be improved by using more and larger diameter traps (Abensperg-Traun and Steven, 1995). Another possibility is to trap over an extended period. Figure 3 shows the cumulative number of species obtained by 22 months of pitfall trapping of an 18 x 18 m plot at Dwellingup, Western Australia. Numbers plateaued at 36 species after the first year of sampling, a figure which fell only slightly short of the richness which is known to exist in this area of habitat (Majer, unpublished data).

Table 1. Number of ant species caught by pitfall trapping expressed as a percentage of those caught by the 'standard' and 'extended' sampling regimes in rehabilitation and native vegetation controls at North Stradbroke, Richards Bay and Trombetas.

Number of ant species in pitfall traps as a percentage of:	North Stradbroke		Richards Bay		Trombetas	
	Rehab.	Control	Rehab.	Control	Rehab.	Control
Standard samples	59.5	47.3	46.4	35.3	41.9	22.3
Extended * samples	56.0	44.0	45.0	32.0	40.0	17.7

*Note that the percentages for the 'extended' samples at Richards Bay and Trombetas are not totally comparable with those from the 'standard' samples since they represent a more limited range of plots.

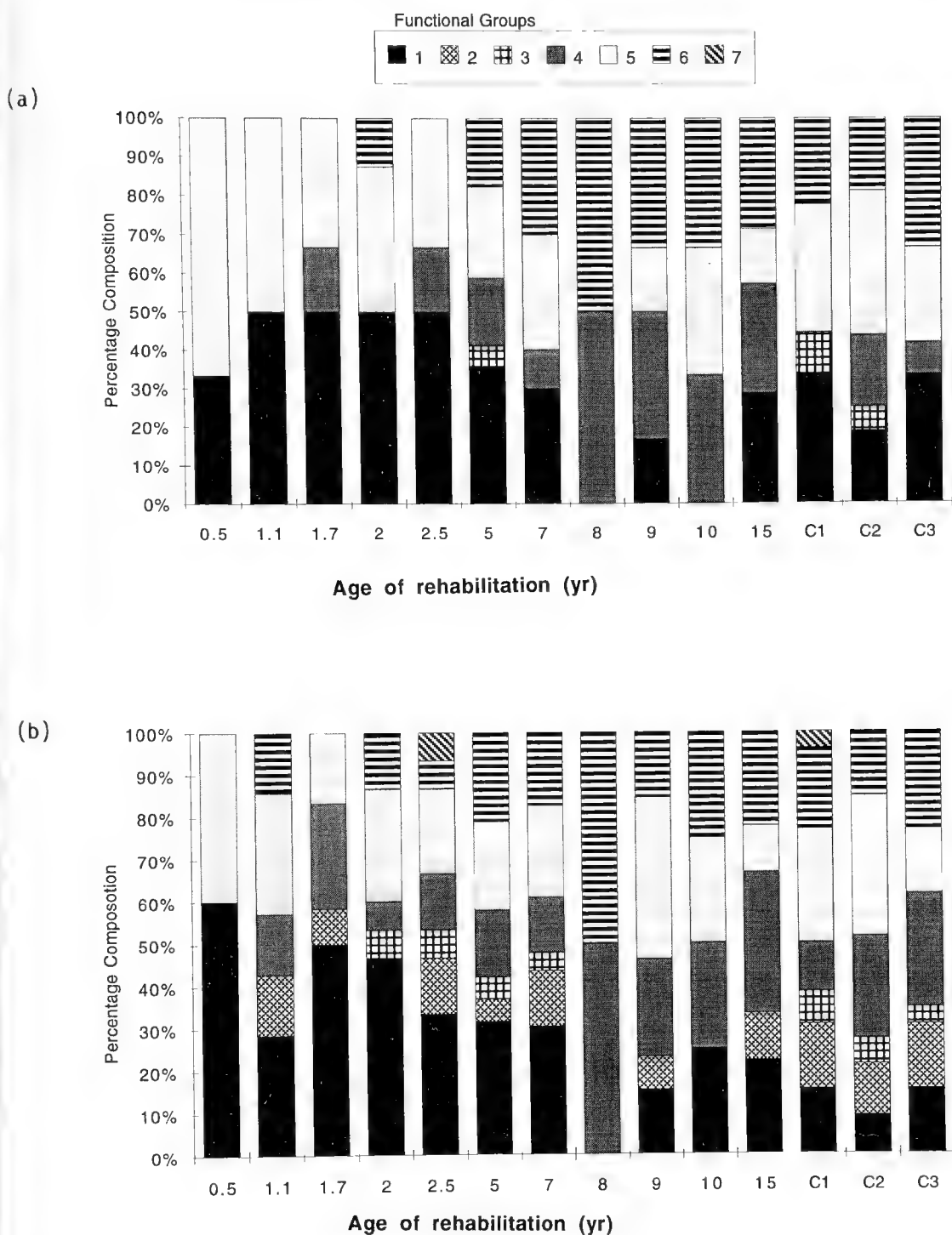


Figure 2. Ant functional group profiles obtained by (a) pitfall trapping and (b) the standard sampling regime in rehabilitation and controls at North Stradbroke Island. Key to ant functional groups: 1 = dominant Dolichoderinae; 2 = subordinate Camponotinae; 3 = climate specialists; 4 = cryptic species; 5 = opportunists; 6 = generalised Myrmicinae; and 7 = large, solitary foragers and/or specialist predators

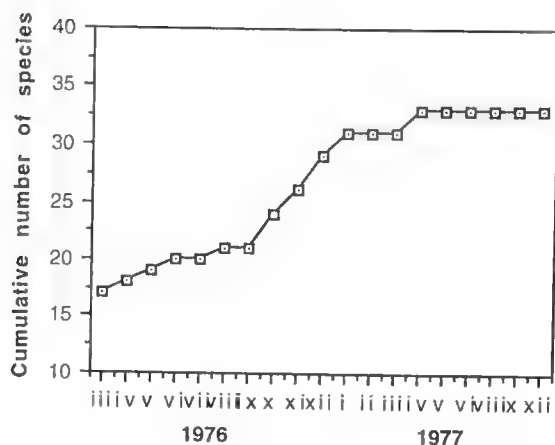


Figure 3. Cumulative number of ant species trapped by 7-day pitfall trapping at monthly intervals in forest at Dwellingup, Western Australia.

Conclusion

In part, the discrepancy between pitfall and standard or extended sample catches is related to the low number of pitfall traps used in the minesite studies; pitfall trapping was never intended to be the main sampling tool. An adequate number of suitably sized pitfall traps are indeed a suitable means of sampling the surface-active ant community in open habitats, although authors who use this approach should specify that the study pertains to the epigeic ant community. However, traps generally undersample the entire ant community in more closed formations. The more structurally complex the habitat, the more serious becomes the problem, with cryptic, hypogaeic, arboreal and rare species being particularly prone to undersampling. Unless the study is specifically of the surface-active ant community, it is not appropriate to rely upon pitfall traps alone.

The purpose of this paper has not been to elucidate the best possible combination of sampling techniques for sampling ant communities. However, in line with the conclusion of Disney et al. (1982) it is recommended that a combination of sampling procedures must be employed if a reasonably complete census of the ant community is to be obtained. A suitable sampling protocol, which involves pitfall trapping, vegetation sweeping and also day and night hand collection has been described in Allen (1989) and Majer (1993). Also, although ants have been used to illustrate the points in this paper, the conclusions and recommendations may well apply to other invertebrate taxa as well.

References

- Abensperg-Traun, M. and Steven, D.E., 1995. The effects of pitfall trap diameter on ant species richness (Hymenoptera: Formicidae) and species composition of the catch in a semi-arid eucalypt woodland. *Australian Journal of Ecology* 20: 282–287.
- Adis, J., 1979. Problems of interpreting arthropod samples with pitfall traps. *Zoologischer Anzeiger* 202: 177–184.
- Allen, N.T., 1989. A methodology for collecting standardised biological data for planning and monitoring reclamation and rehabilitation programmes. Pp. 179–205 in: Majer, J.D. (ed.), *Animals in primary succession: the role of fauna in reclaimed lands*. Cambridge University Press: Cambridge.
- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–357.
- Andersen, A.N., 1991. Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savannah. *Australian Journal of Ecology* 16: 273–279.
- Andersen, A.N., 1993. Ants as indicators of restoration success at a uranium mine in tropical Australia. *Restoration Ecology* 1: 156–167.
- Andersen, A. N. and Yen, A. L., 1985. Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. *Australian Journal of Ecology* 10: 25–30.
- Beattie, A. J. (ed.), 1993. *Rapid biodiversity assessment*. Proceedings of the Biodiversity Assessment Workshop: Macquarie University. 92 pp.
- Burbidge, A.H., Leicester, K., McDavitt, S. and Majer, J.D., 1992. Ants as indicators of disturbance at Yanchep National Park, Western Australia. *Journal of the Royal Society of Western Australia* 75: 89–95.
- Disney, R.H.L., Erzinclioglu, Y.Z., Henshaw, D.J. de C., Howse, D., Unwin, D.M., Withers, P., and Woods, A., 1982. Collecting methods and the adequacy of attempted fauna surveys, with reference to the Diptera. *Field Studies* 5: 607–621.
- Greenslade, P. and Smith, D., 1994. Soil faunal responses to restoration by mulching of degraded semi-arid soils at Lake Murrumbidgee, New South Wales. Pp. 67–69 in: Pankhurst, C.E. (ed.), *Soil biota*. CSIRO: Melbourne.
- Greenslade, P.J.M. and Thompson, C.H., 1981. Ant distribution, vegetation and soil relationships in the Cooloola-Noosa River area, Queensland. Pp. 192–207 in: Gillison, A.N. and Anderson, D.J. (eds), *Vegetation classification in Australia*. CSIRO and ANU Press: Canberra.
- Luff, M.L., 1975. Some problems influencing the efficiency of pitfall traps. *Oecologia* 19: 345–357.

- Majer, J.D., 1977. Preliminary survey of the epigaeic invertebrate fauna with particular reference to ants, in areas of different land use at Dwellingup, Western Australia. *Forest Ecology and Management* 1: 327–34.
- Majer, J.D., 1981. The role of invertebrates in mine-site rehabilitation. *Forests Department of Western Australia Bulletin* 93: 29 pp.
- Majer, J.D., 1983. Ants: bioindicators of minesite rehabilitation land use and land conservation. *Environmental Management* 7: 375–383.
- Majer, J.D., 1985. Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, with particular reference to seed removal. *Australian Journal of Ecology* 10: 31–48.
- Majer, J.D., 1993. Costs of biodiversity assessment. Pp. 35–39 in: Beattie, A.J. (ed.), *Rapid biodiversity assessment*. Proceedings of the Biodiversity Assessment Workshop: Macquarie University.
- Majer, J.D., 1995. Ant recolonisation of rehabilitated bauxite mines at Trombetas, Pará, Brazil. *Journal of Tropical Ecology* 11: 1–17.
- Majer, J.D. and Delabie, J.H.C., 1994. Comparison of the ant communities of annually inundated and terra firme forests at Trombetas in the Brazilian Amazon. *Insectes Sociaux* 41: 343–359.
- Majer, J.D. and de Kock, A.E., 1992. Ant recolonisation of sand mines near Richards Bay, South Africa: an evaluation of progress with rehabilitation. *South African Journal of Science* 88: 31–36.
- Marsh, A.C., 1984. The efficacy of pitfall traps for determining the structure of a desert ant community. *Journal of the Entomological Society of South Africa* 47: 348–352.
- Romero, H. and Jaffe, K., 1989. A comparison of methods for sampling ants (Hymenoptera: Formicidae) in savannas. *Biotropica* 21: 348–352.
- Yeatman, E.M. and Greenslade, P.J.M., 1980. Ants as indicators of habitat in three conservation parks in South Australia. *South Australian Naturalist* 55: 20–30.
- Yen, A.L., Robertson, P. and Bennett, A.F., 1989. A preliminary analysis of patterns of distribution of plant and animal communities in the Victorian mallee. Pp. 54–60 in: Noble, J.C., Joss, P.J. and Jones, G.K. (eds), *The mallee lands: a conservation perspective*. CSIRO: Melbourne.
- York, A., 1994. The long-term effects of fire on forest ant communities: management implications for the conservation of biodiversity. *Memoirs of the Queensland Museum* 36: 231–239.

SPIDERS AS ECOLOGICAL INDICATORS : AN OVERVIEW FOR AUSTRALIA

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Abstract

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Spiders operate as a dominant predator complex which can influence the structure of terrestrial invertebrate communities. The potential use of spiders as indicators of ecological change, amongst a suite of selected taxa, is worthy of further research. Indicator taxa need to be diverse and abundant, readily sampled, functionally significant, and to interact with their environment in a way that can reflect aspects of ecological change. This paper examines the attributes of spiders in terms of these criteria, with an Australian perspective, and proposes the use of families as functional groups to represent divergent foraging strategies and selection of prey types. With such information gain, and reduced impact of the "taxonomic impediment", the cost-benefit of surveys is enhanced to encourage the wider collation of quantitative spider data for management or conservation purposes.

Introduction

Invertebrates have an important role to play in achieving effective conservation and management of biodiversity for three reasons:

1. they dominate fauna in terms of species richness and abundance;
2. they are linked to critical ecological processes and;
3. they can provide quantitative data from small spatial scales (Greenslade and Greenslade, 1984; Yen and Butcher, 1992; Kitching, 1993; Norton, 1994; New, 1995).

As it is impossible to assess all invertebrate taxa, however, the pragmatic approach is to select major taxa on which to focus research efforts (New, 1994).

In the case of using certain faunal groups to reflect and monitor environmental conditions, the term "indicator taxa" is frequently employed (Greenslade and Greenslade, 1984; Andersen, 1990; New, 1995), as here. In the indicator context, observed differences or shifts in the relative abundance of particular taxa can be interpreted to reflect more general ecological attributes or changes in a system. For invertebrates, this has been primarily developed using aquatic or marine taxa to characterise water quality or more specifically, the effect of pollutants (e.g., reviews by Warwick, 1993; Bunn, 1995; Fairweather et al., 1995). For Australian terrestrial invertebrates, parallel approaches have been limited to the established use of ants to evaluate processes of land restoration after

mining (Majer, 1983; Andersen, 1990, ms.). To gain a wider understanding of patterns of biodiversity and ecological change in invertebrate communities, however, a range of taxa need to be adopted (Beattie et al., 1993; Kitching, 1994; New, 1995; Noss, 1990).

The potential of spiders

In selecting a suite of taxa, arguments for choosing those which are functionally important (Yen and Butcher, 1992; New, 1994) are the most convincing. Due to their ecological importance as dominant predators, spiders have been promoted as one of several priority groups for research (Kitching, 1994; Yen, 1995). In terms of their use as ecological indicators, spiders need to fulfil specified criteria, namely they must:

1. be diverse and abundant;
2. be readily sampled;
3. be functionally significant and;
4. interact with their abiotic and biotic environment in a way that can reflect ecological change (Greenslade and Greenslade, 1984; Andersen, 1990; Cranston, 1990; Beattie et al., 1993; Yen, 1995).

The attributes of spiders with respect to these criteria are reviewed below.

1. Diversity and abundance

The order, Araneae, which comprises spiders, is among the six or seven most speciose orders worldwide, with one hectare of tropical forest estimated to contain 300-800 species (Coddington

ton et al., 1991). In Australia, a total of 1876 described species from 430 genera in 68 families has been tallied (Raven, 1988). With notable increases in taxonomic effort over the last eight years, the number of species described has risen by 26% to 2357 (R. Raven, pers. comm., Jan 1996). With only an estimated 30% (Davies, 1985) or 20% (Raven, 1988) of the fauna formally described, these figures clearly demonstrate that Australia is rich in spider taxa. However, the levels of richness are not unmanageable. In the north-east of Tasmania, a coastal heathland survey over 16 months revealed 130 species over a maximum sampled area of 1.2 ha (Churchill, 1993).

Across Australia, spiders have ranged between the most, to the sixth most, abundant invertebrate order from surveys in rainforest and *Eucalyptus* forest canopies using a number of sampling methods (Majer and Recher, 1988; Basset, 1991; Majer et al., 1990; Yen and Lillywhite, 1990; Abbott et al., 1992; Coy et al., 1993; Kitching et al., 1993; Kitching, 1994; Majer et al., 1994). In a subtropical Queensland rainforest tree canopy where spiders dominated the entire arthropod assemblage sampled, they were responsible for 85% of total abundance and 65% of the total biomass (Basset, 1991).

2. Functional significance

As a predator complex, spiders are among the most abundant and important invertebrate consumers across a range of natural and disturbed habitats (Turnbull, 1973; Reichert, 1974; Humphreys, 1988). Levels of predation upon the arthropod biomass of temperate forests have been estimated at 43.8% annual consumption (Moulder and Reichle, 1972). Spiders are often classed as polyphagous (Reichert, 1974; Turner and Polis, 1979), yet, they include specialist predators such as ant mimics and those that simulate pheromones or odours to attract certain prey species (Stowe, 1986; Pollard et al., 1987). Spiders also interact directly as competitors, mutualists, predators, and particularly as prey, with higher order taxa such as birds (Gunnarsson, 1996), fish (Bleckmann and Lotz, 1987), and lizards (Schoener and Spiller, 1987). Consequently, spider assemblages can play a major role in ecosystem function by directly and indirectly regulating the abundance of taxa which determine rates of herbivory, pollination, decomposition, soil production, nutrient cycling or energy flow (Reichert, 1974; Wise, 1993). The value of spiders as indicators relates, therefore, to their being dominant invertebrate predators,

with observed changes in spider faunas having the potential to reflect ecological impacts at lower trophic levels, and across relatively small spatial scales.

3. Ease of sampling

Due to their abundance and diverse behaviours, spiders can be easily sampled by a range of techniques (e.g., Coy et al., 1993). Vagrant ground hunters are readily captured by the cost-effective pitfall trap (Canard, 1982; Merrett and Snazell, 1983; Churchill, 1993). Foliage dwelling taxa are more susceptible to capture by sweep net (Canard, 1982; Churchill, 1993), beating bushes (Canard, 1982; Hatley and MacMahon, 1980); branch clipping (Majer and Recher, 1988; Abbott et al., 1992); chemical knockdown (Majer and Recher, 1988; Yen and Lillywhite, 1990; Kitching et al., 1993) or restricted canopy fogging (Basset, 1991). Spiders that are sedentary and cryptic, or conspicuous by their webs, size or behaviours, are effectively sampled by visual searching and hand collection (Canard, 1982; Coddington et al., 1991; Churchill, 1993). To target spiders in leaf litter, sifting and extraction techniques such as Berlese or Tullgren funnels can provide standardised and quantitative samples (Canard 1979; Coyle, 1981; Coddington et al., 1991).

4. Interaction with their abiotic and biotic environment

For any invertebrate taxon to be considered as an indicator of ecological change, it needs to display a sensitivity to changes in environmental variables which are associated with stress and disturbance (Andersen, 1990; Noss, 1990; New, 1995). Research in the Northern Hemisphere has revealed that habitat structure and/or associated microclimatic factors, which can be altered by many land use practices, strongly influence patterns of spider distribution (reviews by Turnbull, 1973; Uetz, 1991; Wise, 1993). Across environmental and successional gradients the diversity and relative abundance of spider taxa has been shown to exhibit clear shifts (Uetz, 1976; Bultman et al., 1982; Klimes, 1987; Gibson et al., 1992). The relative importance of different variables can change over time (Uetz, 1979), however, with the availability of prey resources another important factor (e.g., Reichert, 1974). In terms of specific responses to environmental disturbance, characteristic changes in spider faunas have been documented in Europe and America for the effects of metal pollution (Bengtsson and Rundgren, 1984;

Clausen, 1986), fire (Merrett, 1976), grazing (Gibson et al., 1992), pasture improvement (Luff and Rushton, 1989) and clearcutting, burning, mowing and plowing (Huhta, 1971; Coyle, 1981; Haskins and Shaddy, 1986). Clearly, the composition of spider communities of different habitat types is affected by certain changes in environmental conditions, the challenge is now to develop a predictive understanding for management purposes.

Australian research

In Australia, comparable research into spider communities has been minimal. In Western Australia, Mawson (1986) studied the richness and diversity of the arachnid fauna in rehabilitated minesites and surrounding undisturbed eucalypt forest in Western Australia. The result included recommendations for improving the rehabilitation process based on the fact that a more complex habitat structure favoured a richer spider fauna. Research beyond community indices, however, is required to evaluate whether Australian spider faunas display patterns of variation in relation to change in key environmental factors.

With the recent expansion of multivariate techniques it is now easier to analyse complex ecological patterns (Gauch, 1982), with indicator properties of invertebrate communities being determined specifically by ordination (Kremen, 1992). Consequently, these techniques have been applied to pitfall trap data derived from a 16 month survey of a coastal heathland spider community in Tasmania, across three nested spatial scales, with the minimum scale 18×18 m (Churchill, 1993, 1995). Correlation coefficients for spider vectors from HMDS ordination (Belbin, 1991), using the Bray Curtis association measure (Bray and Curtis, 1957), revealed strong associations of both spider families and species (correlation coefficients > 0.6 for 85% and 80% vectors, respectively) with patterns of spatial variability across the community (Churchill, 1995). These patterns were strongly associated with changes in habitat structure, particularly the mean cover of plant species. Significant correlations between changes in the abundance of taxa and abiotic variables (e.g., temperature and rainfall) over time were also documented at both the family and species level (Churchill, 1995). These results illustrate that Australian spiders can display a sensitivity to variation in environmental factors, even at the family level. Given that

spider faunas have been shown to respond faster to anthropogenic disturbance than vegetation (Klimes, 1987), they have the potential to reveal early, and more subtle, ecological changes, which characterises the main value of an indicator group (New, 1995).

Spider families as functional groups

The information value of using certain indicator taxa is greatly enhanced if combined with a functional group approach. This approach has been advocated to increase an understanding of the dominant processes which maintain biodiversity (Lambeck, 1992; Walker, 1992) and underlying environmental change (Andersen, 1990). The fact that most spider families differ in their primary foraging mode, has facilitated their classification into broad functional groups (e.g., Canard, 1990; Coyle, 1991). Patterns of relative abundance of key spider families, however, are here proposed as the basis of a functional group approach in Australia given the following:

1. the paucity of ecological knowledge at lower taxonomic levels (Humphreys, 1988);
2. that taxonomic characters at family level have ecological relevance (see below);
3. that prevailing ecological patterns in spider communities can be detected at the family level (Churchill, 1995);
4. an increasing demand for ecologically useful data at finer spatial scales than previously used (Norton, 1994);
5. the need for protocols to assess anthropogenic change on invertebrate faunas that apply to various habitat types and regions (New, 1995);
6. an urgent need to collate this information cost-effectively (New, 1994; Yen, 1993); and
7. the successful development of a parallel approach using ant genera (Andersen, 1990; ms).

As the ecology of Australian spider genera and species is increasingly understood, as for spiders of European heaths (Canard, 1990), this approach can be further refined.

To distinguish families, important morphological characters relate to the size and arrangement of eyes, legs and silk producing organs (e.g., Davies, 1986). These anatomical features directly reflect the perception and use of important environmental components, including prey. In addition, the size of particular taxa and their spatial distribution within a habitat defines the

part of the prey spectrum utilised and hence, their function in the system (Canard, 1990). For example, the family Thomisidae, or crab spiders, have evolved to be ambush hunters, typically cryptic and preying upon small insects attracted to flower heads (Main, 1976). Moreover, the spatial distribution patterns of thomisids are significantly correlated to a high abundance of arthropod pollinators (Turner and Polis, 1979). An observed shift in the relative abundance of a given family, therefore, can indicate more specifically the range of resources being altered by processes of change in the system.

Additional advantages of investigating spider communities *at least* to family level relate to current concerns for rationalising the costs and benefits of surveys (Margules and Austin, 1991; Yen, 1993). In the case of invertebrate surveys, an increasing demand for taxonomic resources to identify genera and species has accentuated the decline in available expertise (Richardson and McKenzie, 1992; Gaston and May, 1992). This issue has been termed the "taxonomic impediment" to effective invertebrate assessment (Cranston, 1990; Kitching, 1993; New, 1994), with which high costs can be associated. Means to circumvent this have focused on development of procedures of "Rapid Biodiversity Assessment" (RBA) where specimens are taken to "morphospecies" or "Recognisable Taxonomic Units" in lieu of specific taxonomic resolution (Cranston and Hillman, 1992; Kitching, 1993; Oliver and Beattie, 1993). The separation of RBA procedures from taxonomy and associated phylogenies (Beattie et al., 1993), however, involves an associated loss of biological and biogeographic data which limits ecological applications.

Alternatively, the use of higher taxonomic levels may suffice for certain survey goals as suggested for stream invertebrate assemblages (Wright et al., 1995). To assess land degradation and restoration processes, Australian ant genera have successfully been used as the basis of a functional group approach (Andersen, 1990). In detecting human impacts on marine faunal communities, responses of higher taxonomic levels have presented an advantage by operating "above the noise of natural variability" (Warwick, 1993). In this context, spiders can offer an additional resilience to "noise" by tolerating notable periods of starvation (Nakamura, 1987), to possibly provide a strong signal when interpreted as an ecological impact lower down the trophic pathway.

To evaluate broad scale ecological patterns in spider assemblages, family level analysis has been suggested (Yen, 1995) and shown to be as effective as the use of species in Tasmanian coastal heath (Churchill, 1995). Since spiders display a sensitivity to variation in environmental parameters, even at the family level, there is a opportunity to investigate, cost-effectively, general responses to various agents of ecological change. Efforts to further refine the data set can be directed at investigating dominant taxa in families which indicate the strongest trends with respect to the specific disturbance, or variables, under study. Relationships between the observed patterns with other biotic/abiotic components can then offer an insight into the key processes behind ecological change for more specific testing.

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References

- Abbott, I., Burbidge, T., Williams, M. and Van Heurck, P., 1992. Arthropod fauna of jarrah (*Eucalyptus marginata*) foliage in Mediterranean forest of Western Australia: Spatial and temporal variation in abundance, biomass, guild structure and species composition. *Australian Journal of Ecology* 17: 263–274.
- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–357.
- Andersen, A.N., ms. Ants as indicators of ecosystem restoration following mining: a functional group approach. *Proceedings of the Conference for Off-Reserve Conservation, Brisbane, 1996.*
- Basset, Y., 1991. The taxonomic composition of the arthropod fauna associated with an Australian rainforest tree. *Australian Journal of Zoology* 39: 171–190.
- Beattie, A.J., Majer, J. and Oliver, I., 1993. Rapid biodiversity assessment: a review. Pp. 4–14 in:

- Rapid Biodiversity Assessment*. Research Unit for Biodiversity and Bioresources, Macquarie University: Sydney.
- Belbin, L., 1991. Semi-strong hybrid scaling, a new ordination algorithm. *Journal of Vegetation Science* 2: 491–496.
- Bengtsson, G. and Rundgren, S., 1984. Ground living invertebrates in metal polluted forest soils. *Ambio* 13(1): 29–33.
- Bleckmann, H. and Lotz, T., 1987. The vertebrate catching behaviour of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). *Animal Behaviour* 35: 641–651.
- Bray, J.R. and Curtis, J.T., 1957. An ordination of the upland forest communities of Wisconsin. *Ecological Monographs* 27: 325–349.
- Bultman, T.L., Uetz, G.W. and Brady, A.R., 1982. A comparison of cursorial spider communities along a successional gradient. *Journal of Arachnology* 10: 23–33.
- Bunn, S.E., 1995. Biological monitoring of water quality in Australia: workshop summary and future directions. *Australian Journal of Ecology* 20: 220–227.
- Canard, A., 1979. Données écologiques sur quelques Aranéides d'une lande sèche armoricaine. *Revue Arachnologique* 2: 303–312.
- Canard, A., 1982. Utilisation comparée de quelques méthodes d'échantillonnage pour l'étude de la distribution des araignées en landes. *Atti Della Società Toscana Scienze Naturali* 88: 84–94.
- Canard, A., 1990. Heathland spider communities, a functional group study. *Acta Zoologica Fennica* 190: 45–50.
- Churchill, T.B., 1993. Effects of sampling methodology on the composition of a Tasmanian coastal heathland spider community. Proceedings of the XIIth International Congress of Arachnology. *Memoirs of the Queensland Museum*. 33(2): 475–481.
- Churchill, T.B., 1995. *Scales of spatial and temporal variation in a Tasmanian heathland spider community*. PhD thesis. Faculty of Environmental Sciences, Griffith University, Brisbane, Qld.
- Clausen, I.H.S., 1986. The use of spiders (Araneae) as ecological indicators. *Bulletin of the British Arachnological Society* 7: 83–86.
- Coddington, J.A., Griswold, C.E., Davila, D.S., Penaranda, E. and Larcher, S.F., 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pp. 44–60 in: Dudley, E.C. (ed.) *The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*. Dioscorides Press: Portland.
- Coy, R., Greenslade, P. and Rounsevell, D., 1993. *A survey of invertebrates in Tasmanian rainforest*. Tasmanian NRCP Technical Report No. 9, Hobart, Tasmania.
- Coyle, F.A., 1981. Effects of clearcutting on the spider community of a Southern Appalachian Forest. *Journal of Arachnology* 9: 285–298.
- Cranston, P.S., 1990. Biomonitoring and invertebrate taxonomy. *Environmental Monitoring and Assessment* 14: 265–273.
- Cranston, P. and Hillman, T., 1992. Rapid assessment of biodiversity using "biological diversity technicians". *Australian Biologist* 5: 144–154.
- Davies, V.T., 1985. Araneomorphae (in part). Pp. 49–125 in: Walton, D.W. (ed.), *Zoological Catalogue of Australia. 3. Arachnida*. Australian Government Printing Service: Canberra.
- Davies, V.T., 1986. *Australian Spiders. Araneae. Collection, preservation and identification*. Queensland Museum Booklet No. 14.
- Fairweather, P., Ludwig, J. and McIntyre, S., 1995. Use of biota to assess water quality: an international conference. *Australian Journal of Ecology* 20(1): 1–220.
- Gaston, K.J. and May, R.M., 1992. Taxonomy of taxonomists. *Nature* 356: 281–282.
- Gauch, H.G., 1982. *Multivariate analysis in community ecology*. Cambridge University Press: Cambridge.
- Gibson, C.W.D., Hamblin, C. and Brown, V.K., 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. *Journal of Applied Ecology* 29: 132–142.
- Greenslade, P. and Greenslade, P.J.M., 1984. Invertebrates and environmental assessment. *Environment and Planning* 3: 13–15.
- Gunnarsson, B., 1996. Bird predation and vegetation structure affecting arthropods in a temperate forest. *Journal of Animal Ecology* 65: 389–397.
- Haskins, M.F. and Shaddy, J.H., 1986. The ecological effects of burning, mowing, and plowing on ground-inhabiting spiders (Araneae) in an old field system. *Journal of Arachnology* 14: 1–13.
- Humphreys, W.F., 1988. The ecology of spiders with special reference to Australia. Pp. 1–22 in: Heather, N.W. and Austin, A.D. (eds), *Australian Arachnology*. The Australian Entomological Society Miscellaneous Publication No. 5.
- Huhta, V., 1971. Succession in spider communities of the forest floor after clearcutting and prescribed burning. *Annales Zoologici Fennici* 8: 483–542.
- Kitching, R.L., 1993. Biodiversity and taxonomy: impediment or opportunity. Pp. 253–268 in: Moritz, C. and Kikkawa, J. (eds), *Conservation Biology in Australia and Oceania*. Surrey Beatty and Sons: Chipping Norton, N.S.W.
- Kitching, R.L., 1994. Biodiversity — political responsibilities and agendas for research and conservation. *Pacific Conservation Biology* 1: 279–283.
- Kitching, R.L., Bergelson, J.M., Lowman, M.D., McIntyre, S. and Carruthers, G., 1993. The biodiversity of arthropods from Australian rainforest canopies: General introduction, methods, sites and ordinal results. *Australian Journal of Ecology* 18: 181–191.
- Kremen, C., 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2: 203–317.

- Lambeck, R.J., 1992. The role of faunal diversity in ecosystem function. Pp.129–148 in: Hobbs, R. (ed.), *Biodiversity of Mediterranean Ecosystems in Australia*. Surrey Beatty and Sons: Sydney.
- Luff, M.L. and Rushton, S.P., 1989. The ground beetle and spider fauna of managed and unimproved upland pasture. *Agriculture, Ecosystems and Environment* 25: 195–205.
- Main, B.Y., 1976. *Spiders*. Collins: Sydney.
- Majer, J.D., 1983. Ants: bioindicators of minesite rehabilitation, land use, and land conservation. *Environmental Management* 7: 375–383.
- Majer, J.D. and Recher, H.F., 1988. Invertebrate communities on Western Australia eucalypts: a comparison of branch clipping and chemical knock-down procedures. *Australian Journal of Ecology* 13: 269–278.
- Majer, J.D., Recher, H.F., Perriman, W.S. and Achuthan, N., 1990. Spatial variation of invertebrate abundance within the canopies of two Australian eucalypt forests. *Studies in Avian Biology* 13: 65–72.
- Majer, J.D., Recher, H.F. and Postle, A.C., 1994. Comparison of arthropod species richness in eastern and western Australian canopies: a contribution to the species number debate. *Memoirs of the Queensland Museum* 36(1): 121–131.
- Margules, C.R. and Austin, M.P. (eds), 1991. *Nature Conservation : cost-effective surveys and data analysis*. CSIRO Australia: Melbourne.
- Mawson, P.R., 1986. A comparative study of arachnid communities in rehabilitated bauxite mines. *Western Australian Institute of Technology, School of Biology Bulletin* 14: 1–46.
- Merrett, P., 1976. Changes in the ground-living spider fauna after heathland fires in Dorset. *Bulletin of the British Arachnological Society* 3: 214–221.
- Merrett, P. and Snazell, R., 1983. A comparison of pitfall trapping and vacuum sampling for assessing spider faunas on heathland at Ashdown Forest, south-east England. *Bulletin of the British Arachnological Society* 6: 1–13.
- Moulder, B.C. and Reichle, D.E., 1972. Significance of spider predation in the energy dynamics of forest floor arthropods communities. *Ecological Monographs* 42: 473–498.
- Nakamura, K., 1987. Hunger and starvation. Pp. 287–295 in: Nentwig, W. (ed), *Ecophysiology of Spiders*. Springer-Verlag: Berlin.
- New, T.R., 1994. Conservation assessment of invertebrate assemblages: Is there a place for global level taxon-focusing? *Memoirs of the Queensland Museum* 36: 153–157.
- New, T.R., 1995. *An introduction to invertebrate conservation biology*. Oxford Science Publications: Oxford.
- Norton, T.W., 1994. An overview of modelling fine-scale variation in environmental regimes in complex landscapes with comments on applications to invertebrate survey, monitoring and conservation. *Memoirs of the Queensland Museum* 36: 173–177.
- Noss, R.F., 1990. Indicators for monitoring biodiversity : a hierarchical approach. *Conservation Biology* 4: 355–364.
- Oliver, I. and Beattie, A.J., 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* 7: 562–568.
- Pollard, S.D., McNab, A.M. and Jackson, R.R., 1987. Communication with chemicals : pheromones and spiders. Pp. 133–141 in: Nentwig, W. (ed), *Ecophysiology of Spiders*. Springer-Verlag: Berlin.
- Raven, R.J., 1988. The current status of Australian spider systematics. Pp. 37–48 in: Austin, A.D. and Heather, N.W. (eds), *Australian Arachnology*. The Australian Entomological Society Miscellaneous Publication No.5.
- Richardson, B.J. and McKenzie, A.M., 1992. Australia's biological collections and those who use them. *Australian Biologist* 5: 19–30.
- Riechert, S.E., 1974. Thoughts on the ecological significance of spiders. *BioScience* 24: 352–356.
- Schoener, T.W. and Spiller, D.A., 1987. Effects of lizards on spider populations: Manipulative reconstruction of a natural experiment. *Science* 236: 949–952.
- Stowe, M.K., 1986. Prey specialisation in the Araneidae. Pp. 101–131 Shear, W. (ed.), *Spiders : webs, behaviour and evolution*. Stanford University Press: California.
- Turnbull, A.L., 1973. Ecology of the true spiders (Araneomorphae). *Annual Review of Entomology* 18: 305–348.
- Turner, M. and Polis, G.A., 1979. Patterns of co-existence in a guild of raptorial spiders. *Australian Journal of Ecology* 48: 509–520.
- Uetz, G.W., 1976. Gradient analysis of spider communities in a streamside forest. *Oecologia* 22: 373–385.
- Uetz, G.W., 1979. The influence of variation in litter habitats on spider communities. *Oecologia* 40: 29–42.
- Uetz, G.W., 1991. Habitat structure and spider foraging. Pp. 325–348 in: Bell, S.S., McCoy, E.D. and Mushinsky, H.R. (eds), *Habitat structure : the physical arrangement of objects in space*. Chapman and Hall: London.
- Walker, B.H., 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18–23.
- Warwick, R., 1993. Environmental impact studies on marine communities : pragmatic considerations. *Australian Journal of Ecology* 18: 63–80.
- Wise, D.H., 1993. *Spiders in ecological webs*. Cambridge University Press: Cambridge.
- Wright, I.A., Chessman, B.C., Fairweather, P.G. and Benson, L.J., 1995. Measuring the impact of sewage effluent on the macroinvertebrate community of an upland stream: The effect of different levels of taxonomic resolution and quantification. *Australian Journal of Ecology* 20: 142–149.
- Yen, A.L., 1993. Some practical issues in rapid biodiversity assessment of invertebrates. Pp. 21–25 in:

- Rapid Biodiversity Assessment*, Research Unit for Biodiversity and Bioresources, Macquarie University: Sydney.
- Yen, A.L., 1995. Australian spiders: an opportunity for conservation. *Records of the Western Australian Museum*. 52: 39-47.
- Yen, A.L. and Butcher, R.J., 1992. Practical conservation of non-marine invertebrates. *Search* 23: 103-105.
- Yen, A.L. and Lillywhite, P.K., 1990. *A preliminary report into the invertebrates collected from the canopy of Tasmanian rainforest trees, with special reference to the Myrtle Beech*. Tasmanian Department of Parks, Wildlife and Heritage (unpublished. Report).

TROPICAL RAINFOREST MYGALOMORPH SPIDERS IN THE AUSTRALIAN DESERT: THE IRONY OF AN ADAPTIVE LEGACY

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Abstract

Main, B.Y., 1997. Tropical rainforest mygalomorph spiders in the Australian desert: the irony of an adaptive legacy. *Memoirs of the Museum of Victoria* 56(2): 339–347.

The semiarid regions of Australia have a high generic diversity of mygalomorph spiders. Several genera are postulated as being “tropical” rainforest genera. Three genera, *Conothele*, *Selenocosmia* and *Cethegus* have been selected for discussion. Persistence of these genera in the arid region is postulated as being due to a combination of natural restriction to relic habitats or those with verisimilitude with rainforest habitats and retention of behavioural attributes which fortuitously fit them to persist. Aspects requiring conservation attention are perceived to be tourism and too frequent fires.

Introduction

The belief in the richness and diversity of life in rainforests, particularly tropical rainforests, forms part of our inherited mythology as reflected in literature and art. No less in biological science, where the diversity of tropical rainforest life provides themes for theory, documentation and estimation: *why* so rich and *how* rich? From the middle of the last century with exploration in the tropics by adventurers and scientists, namely H. W. Bates, Charles Darwin and Alfred Wallace, (and I must mention here the largely overlooked observations of the dominant figure of mid to late nineteenth century spider systematics, Eugene Simon) fascination with this phenomenon has developed into one of the driving themes of evolutionary biology as currently studied — why so rich — what is the mechanism providing this richness and how is it maintained? In the last part of this century, with anxiety about diminution of the biological bank, some biologists have become obsessed with estimating the richness and diversity of life i.e. the array of life at the species level — how many species (Ewing, 1983; Monteith, 1990). The concomitant ideal of documenting this diversity i.e. naming and describing the species and so making a reality of the estimations, is sadly lacking.

In Australia, rainforests (or “closed forests” in some terminologies, e.g., Specht 1981) comprise a small percentage of the landmass. Tropical rainforests are confined to small areas of the northeast coastal region (Specht, 1981, Figure 2; Webb and Tracey, 1981, Figure 1) while wet/dry

seasonal or monsoon rainforest forms small or large pockets in the Kimberley of northern Western Australia (McKenzie, 1991, Figure 3) and the Northern Territory. Dry vine forests in inland and some coastal areas of mid Queensland are also generally included in broad statements about northern or tropical rainforests.

Recently, some zoologists have challenged the “assumption that biodiversity in the tropics is vastly higher than in the temperate zones” (Platnick, 1991) and botanists likewise recognise high diversity outside tropical rainforests, e.g., as in south-western Western Australia (Lamont et al., 1977). In looking at mygalomorph trapdoor spiders it is apparent, and perhaps surprising to those still hungover with the spell generated by the rainforest mythology, that the semiarid regions of Australia are possibly the richest areas at least in terms of generic diversity and behavioural scope. On a broad geographic front, Main (1982) listed 17 of “the 37 or more mygalomorph genera in Australia” as occurring in semiarid and arid regions of Australia. At a smaller scale, a recent study by Main (1996) at Durokoppin in the semiarid Wheatbelt region of Western Australia demonstrated occurrence of at least 25 species in 13 or 14 genera from six families in a small area of less than a square km within a reserve of remnant vegetation of 1030 hectares. It is doubtful whether such taxonomic diversity can be matched in rainforest habitats. Wishart (1993) noted occurrence of eight mygalomorph species in a 95 x 55 m subtropical rainforest remnant at Gerringong in New South Wales. Davies, Gray and other collectors apparently did not find a comparable taxonomic

richness in eastern Australian rainforests during various rainforest surveys, to that found at Durokoppin (see Monteith, and Davies, 1991). Nor did the Bellenden Ker survey in north Queensland produce such a diversity (Monteith and Davies, 1991). Nevertheless it is known from the taxonomic works of Raven (Raven, 1994 and earlier papers), museum collections, my own collection and personal observations that there is indeed a rich mygalomorph fauna in the eastern Australian rainforests including the tropics. Main (1976) also noted 12 species in a short transect across the sclerophyll/rainforest boundary to the *Nothofagus* habitat in Lamington National Park. With later refinements in the taxonomy this number of species and genera would be higher but possibly not as rich as at the Durokoppin site. Surveys in the monsoon rainforests of neither Kakadu (Kikkawa and Monteith, 1980) nor the Kimberley (Main, 1991a) indicated a taxonomic richness to that observed in the semiarid.

Main (1991b) noted 25 genera of the "forty or so" named mygalomorph genera as occurring in "rainforests". However, this number included genera occurring in southern or temperate rainforest while the present discussion is concerned only with those found in tropical rainforests (although of course some of those genera may occur in temperate rainforests as well). The present study notes 26 genera occurring in tropical rainforests (Table 1). Most of these occur also in tall, open forest (mesophytic or sclerophyll forest) but a few are confined to tropical rainforest, e.g., *Masteria* and *Sason*. A few others (e.g., *Kiama*, *Australothele*, *Carrai*, *Migas* and *Plesiothele*) are also confined to rainforest but including southern rainforests and *Nothofagus*.

The theme of this paper concerns those genera which are regarded as being primarily "tropical rainforest genera" but which also extend into semiarid regions. In that such genera are adapted to humid or seasonally humid forest situations it may appear anomalous that some species occur in semiarid/arid regions. I shall now attempt to show that it is the very nature of the spiders' adaptations to tropical rainforest habitats which ironically enables them to live in the desert region. Furthermore I argue (contrary to some of my earlier interpretations) that the spiders, rather than having invaded the desert, have been stranded there following the retreat of their original tropical rainforest landscapes.

Taxonomic diversity of Australian Mygalomorphae

There are ten families of Mygalomorphae currently recognized from Australia (Raven, 1985a). Recent taxonomic revisions have brought the number of mygalomorph genera of mainland Australia and offshore islands and Tasmania to 43 according to Main (1985a) and with those recorded or described since then (Main, 1985b, 1985c, 1986, 1991c; Raven, 1986, 1988, 1994; Churchill and Raven, 1992) plus some reinstated, and one found not to occur in Australia (Raven, 1994), there are now 57 named genera considered valid while there are still several recognised but unnamed genera (pers. obs.).

Tropical rainforest and desert — terminology and distribution

Before discussing the occurrence of rainforest genera in the "desert" some definition of the boundaries of the two habitat regions in the present context is necessary. I use the term rainforest to mean predominantly closed "wet" forest but also to include seasonal i.e. monsoon forest as in the Kimberley and Northern Territory and vine thickets as in Queensland. Thus "tropical rainforest" as used here equates roughly to "closed forest" of Specht (1981, Fig.2).

Northern "open forest woodland" of Specht (1981, Fig. 4) actually embraces many patches of rainforest as documented in McKenzie et al (1991) and patches and gallery forest in the Northern Territory. Thus tropical rainforest in small or large areas is mostly found within the rainfall isohyets of 750mm per annum and above (see Nix, 1981, Figure 10).

"Desert" and semiarid/arid is loosely defined here to encompass that huge interior of Australia with less than 500 mm rainfall per annum, receding to less than 250 mm and 150 mm (see Nix, 1981, Figure 10). The southern boundary accepted in the present context is not as restrictive as that defined as the 250 mm isohyet by Williams and Calaby (1985) and followed by Morton et al (1995, Figure 3.1). However, there are many refugia associated with topographic features throughout the whole of the low rainfall areas of Australia — refugia which can be regarded as harbouring biotic leftovers of an earlier "wetter" climatic regime. Striking examples are found in the valleys of the Central Australian mountains, the gorges of the Hamersley Ranges in Western Australia and around low

hills and granite outcroppings on the subdued landscapes of the Western Australian Plateau and Eyre Peninsula in South Australia. Morton et al. (1995) list 74 refugia in the semiarid and arid region.

Even outside these obvious refugial areas, within the "desert" there are numerous microhabitats which present, in microcosm, habitats that have verisimilitude with tropical rainforests. These persistent, small and large, scattered and isolated refugia preserve certain taxa which by their overall distribution suggest a tropical rainforest origin. However, it is not just that such taxa may have been left *in situ* as the continent has become dryer and wet forest habitats have shrunk. There are also behavioural and life history factors peculiar to the relic genera which favour their persistence.

Furthermore the weather patterns, as well as the vegetation cover and topography of rainforest and "desert" refuges play a big part in maintaining the genera in their peripheral range. Northern rainforest and open forests and woodland regions are dominated by summer rain (Nix, 1981, see Figure 1); the semiarid and desert, south of the tropics by winter rain.

However, as well as winter rain which may be very irregular, the whole of the vast inland also experiences some summer rain associated with isolated thunderstorms and cyclones or monsoonal rains which occasionally extend well south of the tropics. These unpredictable rain events now profoundly affect the persistence of "tropical" elements of the mygalomorph fauna in desert regions.

Tropical rainforest genera — distribution and characteristics

It is now pertinent to state that of the 57 currently accepted mygalomorph genera in Australia, 37 occur in rainforests and of these 26 occur in tropical rainforests (Table 1). Of the latter, many genera also occur in open forest and some have species in drier habitats ranging from woodland to heath and desert. The following seven genera are found *only* in rainforests: *Kiama*, *Australothele*, *Carrai*, *Masteria*, *Plesiothele*, *Migas* and *Sason*. Of these, *Masteria* and *Sason* are restricted to northern i.e. tropical rainforest. Data on rainforest and other relevant habitat distributions to arrive at the information summarised in Table 1 is derived from Main (1985a) where bibliographic sources are given e.g. taxonomic literature associated with species descriptions and later publications (mainly

taxonomic papers but some natural history works) of Churchill and Raven (1992), Gray (1987, 1992), Main (1985b, 1985c, 1986, 1991a, 1991c, 1995, 1996), Raven (1984a, 1984b, 1985b, 1986, 1993, 1994) and to some extent from data with museum collections and finally from my own observations and field records.

I have selected for the present discussion the three genera *Conothele* (Ctenizidae), *Selenocosmia* (Theraphosidae) and *Cethegus* (Dipluridae) which have in common a distribution right across the north i.e. throughout the tropics and primarily in rainforest and which extends widely through other southern habitats within the general "desert" region but they are excluded from the extreme southwest and southeast of the continent. This distribution suggests a tropical origin and possibly a relatively recent entry into Australia, especially for *Conothele* and *Selenocosmia* both of which also occur to the north of Australia, a hypothesis already espoused by Main (1981, 1982). *Cethegus* in having partly and perhaps primarily a tropical and subtropical rainforest distribution (Main, 1960; Raven, 1984c) can similarly be regarded as being a recent denizen of the semiarid. *Aname* (Nemesiidae) and *Missulena* (Actinopodidae) occur widely throughout the continent including the tropical north. *Aname* also occurs in Tasmania from where however *Missulena* is absent. The distribution of *Idiommata* (Barychelidae) may parallel that of the three selected genera and some of its behavioural attributes may similarly account for its broad habitat inclusion. The genus is currently under review by Raven (1994). The remaining genera have more restricted ranges (Table 1).

All those genera occurring in rainforest appear to be dependent on a moist, shaded habitat and species of the three genera also occurring in "desert" areas selected for discussion are restricted to more or less permanently moist habitats as I will show below.

Behavioural and life style characteristics of rainforest "deserticoles"

Most genera which exhibit strong adaptations to desert living are regarded as old, autochthonous Australian genera (Main, 1981). The three "rainforest" genera under discussion persist in the desert firstly by avoiding the desert environment (they are situated in refugia however miniscule), and secondly by retaining a suite of behavioural and life style attributes appropriate to their original rainforest habitat and which

now predispose or fortuitously fit them to survive in generalized arid areas. (In view of the controversy surrounding such terms as pre-adaptation and related contrivances, I am reluctant to add to the confusion by using similar words like "a predisposition" but nevertheless dare to coin the term "fortuitous adaptation"!).

Main (1982) summarised the desert adaptations of mygalomorphs to include morphologi-

cal features which reduce water loss and various combinations of behavioural characteristics such as (1) avoidance of environmental conditions through fossorial habits (2) sedentary life style e.g. burrow site fidelity (3) specialised foraging strategies and seasonal feeding by non-aestivating segments of the population (4) coincidence of reproductive behaviour and dispersion of juveniles with rainy periods (however erratic) (5) extreme longevity of females (6)

Table 1. The 26 genera which occur in tropical rainforest and the extent of their distribution i.e. to include southern areas and whether absent from the southwest and southeast corners of Australia. * = 14 genera which extend into "desert" (arid/semiarid). P = present; sw, southwest, se, south east.

Tropical Rainforest	Widespread	East/Aust only	Absent se/sw
Actinopodidae			
* <i>Missulena</i>	+	—	P
Ctenizidae			
* <i>Conothele</i>	+	—	—
Dipluridae			
* <i>Cethegus</i>	+	—	—
<i>Namirea</i>	—	+	—
<i>Masteria</i>	—	+ne Qld	—
Hexathelidae			
* <i>Hadronyche</i>	—	+& Eyre P	P se
Idiopidae			
* <i>Arbanitis</i>	+	—	P
<i>Cataxia</i>	—	+Qld only	—
<i>Homogona</i>	—	+	P se
Migidae			
<i>Migas</i>	—	+	P se
Nemesiidae			
* <i>Aname</i>	+	—	P
* <i>Chenistonia</i>	+	—	P
* <i>Kwonkan</i>	+w half Aust	—	Psw
<i>Xamiatus</i>	—	+	—
<i>Namea</i>	—	+	—
*? <i>Yilgarnia</i>	+w half Aust	—	—
Theraphosidae			
* <i>Selenocosmia</i>	+	—	—
Barychelidae			
* <i>Idiommata</i>	+	—	Psw
* <i>Synothele</i>	+WA/SA	—	Psw
<i>Trittame</i>	—	+ne	—
<i>Sason</i>	—	+ne	—
<i>Zophorame</i>	—	+ne	—
* <i>Mandjelia</i>	+	—	—
* <i>Ozycrypta</i>	—	+ne/cent	—
<i>Tungari</i>	—	+ne	—
<i>Moruga</i>	+n/trop	—	—

capacity to fast for long periods (7) iteroparous reproduction and (8) limited dispersal capacity in most species.

At the same time these attributes were given as explaining the restricted geographic ranges of many such species which "are tied to particular habitat types categorized by soil/vegetation attributes". Conversely it was pointed out that *Conothele* has a wide geographic range "assisted by its aerial dispersal" and that "the large, aggressive and relatively mobile *Selenocosmia stirlingi* has been able to colonize unstable habitats of the interior".

It is these contrary attributes, plus additional ones but all reminiscent of their rainforest heritage, of *Conothele* and *Selenocosmia* and shared by *Cethegus*, which I wish to emphasise here as being the "fortuitous adaptations" enabling them to live in the desert region. In other words they live *in* the desert but are not *of* the desert.

In considering the "fortuitous adaptations" of *Conothele*, *Selenocosmia* and *Cethegus* the salient ones are probably associated with the following factors:

1. Persistence in relic microhabitats within the arid region;
2. Adoption of microhabitats with verisimilitude with rainforest habitats;
3. Burrow/nest structure;
4. Dispersion method of juveniles;
5. Mobility i.e. capacity to relocate nest/burrow site;
6. Foraging behaviour; and
7. Reproductive behaviour and phenology.

I will now discuss each of the genera in turn to show the relevance of these factors to persistence of the respective taxa as deserticoles.

Conothele

The genus has a wide distribution from Burma, various island groups through New Guinea and Australia (Roewer, 1942; Main, 1981; Raven, 1985). It occurs generally in rainforest and open forest in humid, tropical regions. Nests are usually in the ground but some rainforest species are arboreal and make small cocoon-like tubes with trap doors in bark, thus avoiding inundation in very wet habitats (Main, 1993). Spiders are moderate sized, with a smooth shiny cuticle, very spiny anterior legs and apart from courting males and dispersing juveniles spiders never leave the nest.

(1) In semiarid and arid regions in Australia spiders occur in shaded cliff faces of mountain valleys as in the Hamersley Ranges and other

similar sites in Western Australia and various mountain blocks ("ranges") in Central Australia. Although rocky, these sites due to their geological structure encourage seepage into soil interstices. This dampness combined with shade albeit of shrubs and tussocks provides a habitat that mimics in microcosm an earlier rainforest habitat, of which indeed such sites are relics.

(2) Elsewhere in open country of the dry interior the spiders are found in association with rock tumbles around low hills, and in clay and alluvial soils in small depressions of drainage lines. Thus they occur in either relic microhabitats (valleys of mountain ranges which also retain ancient flora such as *Livistona*) or in habitats with verisimilitude.

(3) The burrow of *Conothele* in most sites is relatively shallow, and lined with a stocking-like tube of tough silk that adheres to a plaster wall and with a tightly-fitting, cap-like silk/soil door. The base of the burrow unless in the process of being deepened is usually fully lined. Thus the burrow acts like a sealed flask — preventing flooding during immersion in wet tropical sites. Secondly this secure tube in flood prone areas in the otherwise dry inland similarly protects the spiders and conversely ameliorates environmental desiccating conditions.

(4) Juveniles disperse aerially (although it is assumed not over great distances) which assists dissemination in rugged terrain or habitats with patchy shrubbery or rocky sites. The method is advantageous in steep sided, rocky gorges as well as open woodland with discontinuous favourable microhabitats.

(5) In unstable creek banks, as in the rainforest (such as in the Kimberley and many northern Australian sites) and steep slopes in open forest e.g., north Queensland and New Guinea, if the burrows are washed over by sheet flooding or even partly dislodged the spiders are securely cocooned because of the sealed stocking structure of the nest and the spiders can relocate or reestablish after being buffeted by sudden erosive conditions.

(6) Spiders are typical sit-and-wait predators and do not fully emerge from the burrow when capturing prey. This possibly limits them to high-prey habitats. However the habitats they occupy would also appear to favour invertebrate density. Spiders do not store rejectamenta in the basally sealed burrow but eject it at the surface (personal observations) which again implies a certain transitoriness unlike the extreme sedentary nature of most arid adapted species which

are more vulnerable to sudden disturbance of habitat (and habitually store rejectamenta).

(7) Little is known about the reproductive behaviour of the genus other than that wandering of males and juvenile dispersion is linked with rainy periods (at whatever season).

"*Selenocosmia*"

The genus occurs from India to New Guinea and Australia (Roewer, 1942). However the family representatives of Theraphosidae in Australia require taxonomic revision and the generic category "*Selenocosmia*" is loosely applied in the present context. Schmidt (1995) transferred the Australian species of *Selenocosmia* to *Phlogius* in which genus early species were originally placed. The spiders are very large and hairy with long legs. Spiders make very deep burrows.

(1), (2) and (3) While it is difficult to identify "desert" sites of a relictual nature, most habitats (throughout the inland in various States) certainly have verisimilitude in that they are lowlying, wet or seasonally wet, in relatively unstable situations and may be flooded during the rainy season. Because the spiders are already adjusted to inundation of burrows (e.g. in seasonal "swamps" or "bogs" in the Kimberley) inundation in flood prone, arid flats is not inimical. It is possible that the very deep burrows maintain air pockets. Also the furriness of the spiders' bodies encourages formation of an enclosing air bubble thus spiders may be immersed without drowning. The earliest records of the habitat of the "barking" or "whistling" spider, *Selenocosmia stirlingi* is in the classic account of the spider in *The Report of The Horn Expedition* (Spencer, 1896) where the spiders are noted as occurring in "grassy flats amongst low hills". These would be the swales between the ranges and sand dunes, low lying areas subject to sheet flooding and temporary boggy conditions following intermittent rain. They in this way resemble seasonal wet/dry depressions where other species occur in the Kimberley and north Queensland (pers. obs.)

(4) Little is known about juvenile dispersion other than that it is assumed spiderlings scatter freely on the ground (Kotzman, 1986).

(5) Spiders appear to be readily mobile and there is some evidence (Kotzman, 1986 and pers. obs.) that spiders move sites at least in arid habitats.

(6) Spiders may lay an entrapping mesh of web

around the burrow entrance. In addition they emerge to hunt or actively chase prey.

(7) Spiders are mostly summer breeding, which in the monsoon forests at least ties in with the "wet". In the arid region spiders are more opportunistic, males taking advantage of irregular summer rains to wander. Longevity of females enables individual spiders to forego breeding during drought years while persisting as a population (a common strategy of arid adapted mygalomorphs (Main, 1976, 1978)).

Cethegus

Commonly called "curtain web spiders", these spiders have long spinnerets (associated with their profuse web building). They are moderately sized, hairy, with relatively long legs which tend to turn backwards at the tips. Although they are web weavers, they are remarkably agile on the ground and can move very quickly. In rainforests the spiders make diffuse silk tubes amongst rocks, in logs or on irregular cliff faces. In monsoon forest they frequently occur in the rocky river beds. These are inundated during the "wet" when the spiders are possibly washed out or enclosed in their flocculent silk and temporarily submerged. There is no data to suggest that spiders leave their burrows and climb trees or vegetation prior to the onset of inundation as occurs with some South American *Ischnothelines* (Hofer, 1990) but this is another possibility. However, their taxonomic affinity with this group suggests also a behavioural flexibility which may include a predisposition to transient web siting.

(1) Like *Conothele*, *Cethegus* often occurs in rocky cliff faces which determine seepage of moisture to the surface or in cracks in "relict" habitats in gorges and valleys in the arid region.

(2) and (3) A notable behaviour in open, semi-arid habitats is that spiders site the burrow and curtain web against a supporting butt of a shrub or small tree which secondarily provides the benefit of harvesting water into the burrow which ramifies the soil amongst the roots. Water harvesting by trees and shrubs in arid areas is a well known phenomenon (Slatyer, 1965; Nulsen et al., 1986).

(4) Juveniles are aurally dispersed (Main, 1995 and unpublished records).

(5) Spiders appear to relocate nest sites in unstable rainforest habitats (inferred behaviour) (Main, 1993) and certainly relocate (due to rain damaged webs and burrows) after rain in semi-arid habitats. The relocation of numerous nests

has been documented at Durokoppin (Main, 1993, pers. obs., unpublished records).

(6) Spiders ensnare prey in their webs and take a variety of crawling and flying insects and other arthropods. The web probably ensnares a higher prey take than that available to typical sit-and-wait trapdoor spiders.

(7) As with other genera reproductive behaviour and dispersion is opportunistic depending on seasonal or irregular rain. However there is some evidence (pers. records) that males develop more rapidly than most mygalomorph species. Precocious development, as argued by Main (1991) would mean lower mortality due to shortened exposure to environmental hazards and thereby increased surety of reproduction in unstable, flood prone (tropical) and climatically unpredictable (arid) habitats.

Discussion

The three tropical rainforest genera *Conothele*, *Cethegus* and *Selenocosmia* have been shown from the taxonomic literature, museum collections and personal observations and collections to be also widely distributed throughout Australia, including the low rainfall areas but exclusive of the mesophytic southwest and south east forests and southern coastal regions. Evidence from natural history observations and distribution records substantiates the hypothesis that these genera survive in the broad semiarid to desert region, not by having evolved specific adaptations to the desert but by retaining adaptations which primarily fitted them to the instability of wet (even if only seasonally wet) tropical habitats.

At the same time the spiders do not appear to have expanded their habitat range but rather to have become restricted to relic rainforest habitats or to "newer" microhabitats which exhibit verisimilitude, at least seasonally, with wet tropical habitats. Even where *Cethegus* occurs in the dry, open "desert" country of the Western Australian Goldfields, which appears to have little resemblance to tropical rainforest, there are reminders of an earlier, wetter scenario in the scattered presence of the kurrajong trees, *Brachychiton gregorii*. Cycads and the *Livistona* palms persist in gorges of the Central Australian Ranges and the latter in some isolated gorges in northwestern Australia (Humphreys et al., 1990). Nor do these spiders demonstrate specific behavioural specialisations comparable to those of the endemic, autochthonous genera. Thus it seems that the apparent rainforest

"deserticoles", by virtue of retaining their rainforest life style and repertoire of adaptations (transmuted as "fortuitous adaptations") are masquerading as "deserticoles".

In the light of this the implications for conservation management are obvious. Especial care needs to be directed to preserving intact relic sites in gorges and less easily identifiable sites with "verisimilitude". In that rainforest habitats are generally not fire prone, relic habitats within the arid zone need to be protected to prevent an edge erosion by fires. With the present infiltration of tourism (see also Morton et al., 1995) that is oriented to once off, casual, sight seeing visitations, the increasing danger of disturbance simply by people pressure to many biologically resilient but physically brittle sites is inevitable. And this is quite apart from the inimical effects of too frequent fires upsetting the habitats and faunal populations.

The spiders *cannot* be the only potential victims — but they are surely the silent advocates for a whole suite of invertebrates.

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References

- Churchill, T.B. and Raven, R.J., 1992. Systematics of the intertidal trapdoor spider genus *Idiactis* (Mygalomorphae: Barychelidae) in the western Pacific with a new genus from the northeast. *Memoirs of the Queensland Museum* 32 (1): 9–30.
- Ewing, T.L., 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. Pp. 59–75 in: Sutton, S.L., Whitmore, T.C. and Chadwick, A.C. (eds). Blackwell: Edinburgh.
- Gray, M.R., 1987. Distribution of the funnel web spiders. Pp. 313–321 in: Covacevich, J., Davie, P. and Pearn, P. (eds). *Toxic plants and animals — a guide for Australia*. Queensland Museum: Brisbane.

- Gray, M.R., 1992. Funnel-webs: separating fact from fiction. *Australian Natural History* 24(3): 32–39.
- Hofer, H., 1990. The spider community (Araneae) of a Central Amazonian blackwater inundation forest (igapo). *Acta Zoologica Fennica* 190: 173–179.
- Humphreys, W.F., Brooks, R.D. and Bine, B., 1990. Rediscovery of the palm *Livistona alfredii* on North West cape Peninsula. *Records of the Western Australian Museum* 14: 647–650.
- Kikkawa, J. and Monteith, G.B., 1980. *Animal ecology of monsoon forests of the Kakadu region, Northern Territory*. Unpublished report to Australian National Parks and Wildlife Service: Canberra, ACT.
- Kotzman, M., 1986. *Aspects of the biology of Selenocosmia stirlingi Hogg (Araneae, Theraphosidae)*. Ph.D. Thesis, Monash University, Melbourne.
- Lamont, B.B., Downes, S. and Fox, J.E.D., 1977. Important value curves and diversity indices applied to a species-rich heathland in Western Australia. *Nature* 265: 438–441.
- McKenzie, N. L., 1991. An ecological survey of tropical rainforests in Western Australia: background and methods. Pp. 1–26 in: McKenzie, N.L., Johnston, R.B. and Kendrick, P.G. (eds), *Kimberley rainforests of Australia*. Surrey Beatty and Sons: Chipping Norton, New South Wales.
- McKenzie, N.L., Johnston, R.B. and Kendrick, P.G., 1991. *Kimberley rainforests of Australia*. Surrey Beatty and Sons: Chipping Norton, New South Wales.
- Main, B.Y., 1960. The genus *Cethegus* Thorell (Mygalomorphae: Macrothelinae). *Journal of the Royal Society of Western Australia* 43(1): 30–34.
- Main, B.Y., 1976. *Spiders*. Collins: Sydney.
- Main, B.Y., 1978. Biology of the arid-adapted Australian trap-door spider *Anidiops villosus* (Rainbow). *Bulletin of the British Arachnological Society* 4(4): 161–175.
- Main, B.Y., 1981. Eco-evolutionary radiation of mygalomorph spiders in Australia. Pp. 853–872 in: Keast, A. (ed.), *Ecological biogeography of Australia*. W. Junk: The Hague.
- Main, B.Y., 1982. Adaptations to arid habitats by mygalomorph spiders. Pp. 273–283 in: Barker, W.R. and Greenslade, P.J.M. (eds), *Evolution of the flora and fauna of arid Australia*. Peacock Publications: Frewville, South Australia.
- Main, B.Y., 1985a. Mygalomorphae. Pp. 1–48 in: Walton, D.W. (ed.), *Zoological Catalogue, vol. 3, Arachnida*. Australian Government Publishing Service, Canberra: ACT.
- Main, B.Y., 1985b. Further studies on Australian Diplurinae: a review of the genera of the Teylini (Araneae: Mygalomorphae: Dipluridae). *Australian Journal of Zoology* 33: 743–759.
- Main, B.Y., 1985c. Further studies on the systematics of ctenizid trapdoor spiders: a review of the Australian genera (Araneae: Mygalomorphae: Ctenizidae). *Australian Journal of Zoology, Supplementary Series* 108: 1–84.
- Main, B.Y., 1986. Further studies on the systematics of Australian Diplurinae (Araneae: Mygalomorphae: Dipluridae): a new genus from south-western Australia. *Records of the Western Australian Museum* 12 (4): 395–402.
- Main, B.Y., 1990. Dwarf males in mygalomorph spiders: adaptation to environmental hazards. *Acta Zoologica Fennica* 190: 273–278.
- Main, B.Y., 1991a. Kimberley spiders: rainforest strongholds. Pp. 271–294 in: McKenzie, N.L., Johnston, R.B. and Kendrick, P.G. (eds), *Kimberley rainforests*. Surrey Beatty and Sons: Chipping Norton, New South Wales.
- Main, B.Y., 1991b. Trapdoor spiders. Pp. 363–364 in: Werren, G. and Kershaw, P. (eds), *The rainforest legacy*. Australian Government Publishing Service, Canberra, ACT.
- Main, B.Y., 1991c. Occurrence of the trapdoor spider *Moggridgea* in Australia with descriptions of two new species (Araneae: Mygalomorphae: Migidae). *Journal of Natural History* 25: 383–397.
- Main, B.Y., 1993. From flood avoidance to foraging: adaptive shifts in trapdoor spider behaviour. *Memoirs of the Queensland Museum* 33 (2): 599–606.
- Main, B.Y., 1995. Survival of trapdoor spiders during and after fire. *Calm Science Supplement* 4: 214–215.
- Main, B.Y., 1996. Microcosmic biogeography: trapdoor spiders in a time warp at Durokoppin. Pp. 163–171 in: Hopper, S.D., Chappill, J., Harvey, M. S. and George, A. S. (eds), *Gondwanan heritage: past, present and future of the Western Australian biota*. Surrey Beatty and Sons, Chipping Norton, New South Wales.
- Monteith, G. 1990. Rainforest insects: biodiversity, biogeostimation, or just hand-waving? *Myrmecia* 26 (3): 93–95.
- Monteith, G.B. and Davies, V.T., 1991. Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. Pp. 345–362 in: Werren, G. and Kershaw, P. (eds), *The rainforest legacy, 2 — Flora and fauna of the rainforests*. Australian Government Publishing Service: Canberra.
- Morton, S.R., Short, J. and Barker, R.D., 1995. Refugia for biological diversity in arid and semi-arid Australia. *Biodiversity Series, Paper No. 4*. Biodiversity Unit, Department of Environment Sport and Territories: Canberra, ACT.
- Nulsen, R.A., Bligh, K.J., Baxter, I.N., Solin, E.J. and Imrie, D.H., 1986. The fate of rainfall in a mallee and heath vegetated catchment in southern Western Australia. *Australian Journal of Ecology* 11: 361–371.
- Nix, H.A., 1981. The environment of Terra Australis. Pp. 103–133 in: Keast, A. (ed.), *Ecological biogeography of Australia*. W. Junk: The Hague.
- Raven, R.J., 1984a. A revision of the *Aname maculata* species group (Dipluridae, Araneae) with notes on biogeography. *Journal of Arachnology* 12: 177–193.

- Raven, R.J., 1984b. Systematics and biogeography of the mygalomorph spider family Migidae (Araneae) in Australia. *Australian Journal of Zoology* 32: 379–390.
- Raven, R.J., 1984c. Systematics of the Australian Curtain-web spiders (Ischnothelinae: Dipluridae: Chelicerata). *Australian Journal of Zoology, Supplementary Series* 93: 1–102.
- Raven, R.J., 1985a. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. *Bulletin of the American Museum of Natural History* 182 (1): 1–180.
- Raven, R.J., 1985b. A revision of the *Aname pallida* species-group in northern Australia (Anaminae: Nemesiidae: Araneae). *Australian Journal of Zoology* 33: 377–409.
- Raven, R.J., 1986. A revision of the spider genus *Sason* Simon (Sasoninae, Barychelidae, Mygalomorphae) and its historical biogeography. *Journal of Arachnology* 14: 47–70.
- Raven, R.J., 1988. A revision of the mygalomorph spider genus *Idioctis* (Araneae, Barychelidae). *American Museum Novitates* No. 2929: 1–14.
- Raven, R.J., 1993. The biodiversity of Australian mygalomorph spiders. I. Two new species of *Namirea* (Araneae: Dipluridae). *Memoirs of the Queensland Museum* 34 (1): 81–88.
- Raven, R.J., 1994. Mygalomorph spiders of the Barychelidae in Australia and the western Pacific. *Memoirs of the Queensland Museum* 35 (2): 291–706.
- Roewer, C.F., 1942. *Katalog der Araneae, Band I*. Paul Budy: Bremen.
- Schmidt, G., 1995. Gehoren "*Selenocosmia*" *crassipes* (L. Koch, 1873) und "*Selenocosmia stirlingi*" Hogg, 1901 (Araneida: Theraphosidae: Selenocosmiinae) wirklich zu *Selenocosmia* Ausserer, 1871? *Arachnologisches Magazin* 3(11): 1–12.
- Slatyer, R.O., 1965. Measurements of precipitation interception by an arid zone plant community (*Acacia aneura* F. Muell.) *Arid Zone Research* 25: 181–192.
- Specht, R.L., 1981. Major vegetation formations in Australia. Pp. 163–297 in: Keast, A. (ed.), *Ecological biogeography in Australia*. W. Junk: The Hague.
- Spencer, B., 1896. On the presence and structure of a stridulating organ in *Phlogius* (*Phrictus*) *crassipes*. Pp. 413–415 in: Spencer, B. (ed.), *Report on the work of the Horn Scientific Expedition to Central Australia. Part II, Zoology*. Dulau: London and Melville, Mullen and Slade: Melbourne.
- Webb, L.J. and Tracey, J.G., 1981. Australian rainforests: Patterns and change. Pp. 605–694 in: Keast, A. (ed.), *Ecological biogeography in Australia*. W. Junk: The Hague.
- Wishart, G.F.C., 1993. The biology of spiders and phenology of wandering males in a forest remnant (Araneae: Mygalomorphae). *Memoirs of the Queensland Museum* 33(2): 675–680.

PROSPECTS FOR THE RAPID ASSESSMENT OF TERRESTRIAL
INVERTEBRATE BIODIVERSITY

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Abstract

Trueman, J.W.H. and Cranston, P.S., 1997. Prospects for the rapid assessment of terrestrial invertebrate biodiversity. *Memoirs of the Museum of Victoria* 56(2): 349-354.

Calls for rapid biodiversity assessment (RBA) have not always been explicit about what is meant by Rapid or by Biodiversity Assessment. Rapid can imply (i) a need for immediate results, (ii) speedy field survey, (iii) the use of diversity measures based on taxonomic identification to categories above the species level, or (iv) fast (?) post-field techniques such as the use of recognisable taxonomic units (RTU) in place of species-level identification. Some policy documents confound more than one meaning in a single statement.

Biodiversity, in invertebrate survey work, has been taken to mean species richness, though the significance of such a measure for conservation evaluation purposes has not been established.

This paper reports on a rapid (fast), rapid (short sampling time) comparison of rapid (higher taxon and morpho-species) versus non-rapid (species level) approaches to species-richness assay at five disparate sites in north-east Tasmania. The study has implications for Rapid Biodiversity Assessment in several of its meanings.

Introduction

The term Rapid Biodiversity Assessment (RBA) has become associated with at least four different meanings of rapid:

1. that answers to biodiversity questions are needed quickly;
2. that field surveys should be done speedily using multidisciplinary teams to cover many taxa simultaneously;
3. that diversity measures may be based on traditional taxonomic categories above the species level; and
4. that species richness measures may be based on Recognisable Taxonomic Units (RTU) in place of conventional specimen identification.

Rapid *sensu* fast is the meaning commonly found in government policy documents and the like. For example, the Rio Convention (UN Convention on Biological Diversity) calls for signatory countries to undertake comprehensive biodiversity assessments within two years. Rapid *sensu* quick survey using a multidisciplinary team has been popularised by Conservation International, Inc., which sends such teams to remote, previously unstudied sites to provide a detailed inventory of the flora and fauna to be found there (see, e.g., Conservation International, 1991). Rapid *sensu* the use of

higher taxonomic categories and of RTU correspond to the "Ordinal RBA" and "Basic RBA" of Beattie et al. (1993), and are Australian meanings not in current use elsewhere.

The current draft National Strategy for the Conservation of Australia's Biological Diversity (DEST, 1995) conflates three of the four meanings of Rapid. Section 4.1.2 of that document calls for action to

... establish a joint Commonwealth and State and Territory program to carry out rapid assessment of Australia's biological diversity. (From the context, rapid in sense 1.)

but characterises "rapid biological diversity assessment" as

a range of methods that facilitate rapid field survey work and classification. The fieldwork normally involves a multidisciplinary team, including experienced field scientists and people with local knowledge, in surveying component groups representative of biological diversity. (rapid: sense 2)

which leads the survey team to

quantify the variety of organisms collected by classifying them into recognisable taxonomic units. (rapid: sense 4)

The document asserts that RTU techniques will "overcome the large time requirements of formal classification", but this claim currently is unproven. RTU methods may well be as slow or

slower than conventional identification using published keys when many taxa are compared across many samples simultaneously.

In the literature on Rapid Biodiversity Assessment as it applies to invertebrate taxa and to rapid in senses 3 and 4, "Biodiversity" has come to be equated with site species richness. Given that many species remain undescribed and that the biology of most others is poorly known, neither intra-species variation (genetic diversity) nor species interactions (ecosystem diversity) are measurable for most invertebrate taxa. Species diversity thus is, arguably, the one aspect of biodiversity which can be reliably surveyed. However, the usefulness of the resulting site species richness measures, especially in the context of conservation decisions, is questionable.

Differences in site species richness clearly are relevant in comparative studies in ecology and evolution. Their significance in any other context has yet to be established. Rapid Biodiversity Assessment is concerned almost entirely with conservation and land management decisions, and in this context species number as a measure of site diversity would appear to be of minor importance. Representativeness and complementarity amongst conserved areas, the 'keystone' attributes of species or ecosystems, the ecological products of species and areas, ecosystem fragility, current or forecast threat and the likely results of possible management interventions appear to be of greater significance than any count or comparison of species number across sites.

Site-based study

We set out to examine several issues in RBA as it applies to terrestrial invertebrates, using literature review supplemented by a small site-based study. Amongst the questions to be addressed were

1. the prospects for establishing the relative species richness of sites using fast field survey;
2. the prospects for obtaining site biodiversity rankings from higher-taxon counts;
3. the prospects for obtaining species number estimates using RTU;
4. the relative time budgets, information content and practicality of RTU-based versus conventional post-field procedures; and
5. the prospects for identifying predictor sets: taxa which predict site species richness.

Details of the field survey were reported in Trueman and Cranston (1994) (copies available from the authors). Findings re item 5 are discussed in an accompanying paper (Cranston and Trueman, this volume). In the current paper we summarise our observations and field-survey findings as they relate to items 1–4.

Field methods

Surveys were conducted at five sites in north-eastern Tasmania. Sites were established in wet sclerophyll forest (3 km NE of Weldborough: 41°10'S, 147°54'E), dry eucalypt forest (20 km E of above site: 41°09'S, 148°08'E), coastal heathland (Eddystone Point, Mount William National Park: 41°00'S, 148°19'E), periodically inundated heath (Mount William National Park: 41°02'S, 148°15'E) and buttongrass swamp (18 km N of St Helens: 41°12'S, 148°10'E.) We refer to these as sites A–E respectively.

The sites were selected to be visually and vegetatively different from each other. We reasoned that if very disparate sites such as these are not consistently given the same rank ordering on some measure of biodiversity, that measure will not be suitable for comparing more closely similar sites.

Sites were sampled three times at three-monthly intervals. Ten pitfall traps and two yellow-pan traps of standard design were set at each site in each of February, May and August, 1993. (Trap design details are given in the accompanying paper.) The pitfalls were opened for 1 week and the yellow-pans for 24 hours on each sampling occasion. In February only, ten small pitfall traps of a different design (McCartney bottles part filled with 75–80% ethanol, Greenslade and Greenslade, 1971) were set and equal-effort vacuum samples were taken. Yellow-pan traps on a black background were set in August for comparison against conventional traps. Leaf litter samples were taken at the two forested sites on each sampling occasion, and arthropods extracted from the samples over a 1 week period in Tullgren funnels.

All animals from each sample were picked and sorted to ordinal level (insects) or to phylum or other appropriate category (other arthropods). Specimens were counted, identified to RTU by project personnel not expert in the relevant taxonomic group, prepared and mounted (as necessary) for formal identification, and identified by expert taxonomists where available. Records were kept of the times taken at each stage of each

process. All comparisons of species richness, etc., are based on comparable sampling procedures

Field survey results

Table 1 compares fieldwork times and post-field times for our modest sample survey. We recovered 41137 specimens of which 47% were mites, 29% Collembola, 18% insects and 6% other taxa. The ratio of post-field time to field time was approximately 3.5:1 for an incomplete identification of the taxa present in the samples. This is comparable with times recorded in previous partial invertebrate surveys (e.g., Codrington et al., 1991). It emphasises the scope for fast post-field procedures in producing rapid (sense 1) results.

Table 1. Overall time allocation (person-hours)

Fieldwork (elapsed)	390
Sorting	590
Counting/recording	200
Specimen preparation*	250
Taxonomic Identification**	332
	1762

* Not all taxa were prepared for identification, and then not all by project personnel as distinct from expert consultant taxonomists. The figure of 250 hours includes partial preparation of all samples but full preparation only of adult Coleoptera and adult Diptera.

** Not all taxa were identified by taxonomists, as for some groups no taxonomist was available within the time frame of the project. The figure of 332 hours covers myriapods, spiders, collembolans, thrips, adult beetles, adult flies (to family), ants, and non-ant hymenopterans. For Collembola and non-ant Hymenoptera only the February samples were processed.

Table 2 compares our sites based on identified species (including in litter samples from the two sites where litter was present). The figures given are rank order of sites from 1 (most speciose) to 5 (least speciose). It is immediately apparent that relative species richness varies according to which taxa are being sampled.

We found clear evidence that the spectrum of arthropods captured is sensitive to choice of trapping method. For example, 65% of non-ant Hymenoptera specimens and 41% of adult Diptera specimens were taken in yellow-pan traps while 98% of pseudoscorpions occurred in the

Table 2. Site ranking by species richness.

	Site*				
	A	B	C	D	E
Diplopoda	1	2	3	4	4
Chilopoda	2	1	2	4	4
Spiders	2	1	3	4	5
Collembola (Feb)	1	2	3	5	4
Thysanoptera	5	1	2	3	3
Coleoptera	1	2	3	4	5
Diptera (fams)	5	3	1	3	2
Ants	5	2	1	3	4
Non-ant Hymenoptera (Feb)	2	1	3	5	3
All taxa	2	1	3	5	4

* Sites: A, wet sclerophyll; B, dry sclerophyll, C, coastal heath; D, wet heath; E, buttongrass.

leaf litter samples. Such gross differences in catch are to be expected for these taxa. Less expected were major differences based on trap design. We found large and consistent differences in species composition between samples from small and standard pitfall traps and from yellow-pan traps with and without a black background sheet. Amphipods, spiders, opilionines, scorpions, centipedes, millipedes, grasshoppers and adult moths were taken almost exclusively in large pitfall traps not in small, while isopods, earwigs and larval lepidopterans were taken in small traps not in large. At site B five times as many Diptera were taken in yellow-pans with black background as in the standard design trap while at site E, with a different faunal composition, these proportions were reversed.

Although in part such differences may reflect small sampling effects, the observed distribution of lower level taxa (families, genera) across trap type suggests that trap design has a real influence on the spectrum of arthropods captured. Clearly, any biodiversity survey which seeks to sample the entire range of species at a site must employ a range of collecting methods, and inter-site comparison will require that a common set of methods be employed across sites.

We found evidence that a short time frame, generalist trapping program of the type we employed gives a sufficient sample for the estimation of species richness in some taxa but not others. Species accumulation curves suggested that small ground-dwelling animals such as Collembola and small beetles were sampled sufficiently to estimate actual species presence (as

opposed to species collected) using extrapolative techniques such as those described in Heltsche and Forrester (1983) and employed by Coddington et al (1991). Larger animals (eg carabid beetles), animals with naturally clumped distributions within each site (eg, ants), or taxa comprising many species each represented by few individuals (eg, spiders) were insufficiently represented for accurate species number estimation. The implication is that a field survey several times more intensive than ours, or else special sampling techniques directed at individual taxa, would be necessary to adequately sample some parts of the fauna for site species richness.

Table 3 shows the results of a site ranking exercise based on "Ordinal RBA" (rapid assessment in the third sense of "rapid"). Many ordinal measures are possible. We chose to use taxonomic categories to which we could allocate specimens with minimal error. For us this corresponded to the family/ order/ higher-level groupings used in our initial sort. Persons with greater knowledge of some taxa would, no doubt, be able to define and use a different set of categories.

Table 3. Site ranking by the numbers of specimens in each "order"; large pitfall samples only

	Site*				
	A	B	C	D	E
Amphipoda	1	2	3	5	4
Acari	3	2	1	4	5
Spiders	3	1	2	4	5
Opilionida	2	3	1	4	5
Chilopoda	3	2	1	4	4
Diplopoda	3	2	1	4	4
Collembola	2	1	3	5	4
Orthoptera	3	5	3	1	2
Hemiptera	1	5	2	4	3
Thysanoptera	4	5	1	3	2
Coleoptera	1	2	3	4	5
Diptera	3	2	1	4	5
Non-ant Hymenoptera	3	1	1	4	5
Ants	5	3	1	2	4
All groups*	3	2	1	4	5

*ie, an average across "orders" when each is given equal weight. Collembola and Acari would dominate the result if equal weight were given to each specimen.

A comparison of sites on the basis of which "orders" are present was uninformative because all orders were minimally present at all sites on all sampling occasions. Instead we examined the pattern of specimen abundance by "order". Table 3 shows site rankings based on the catch from large pitfall traps. As with the previous table the site ranking varies depending which taxon is surveyed. The average of the rankings, 3-2-1-4-5 for sites A-E respectively, matches that of Acari and Diptera. This pattern applies only to the large pitfall trap samples and it is unstable over time. For example, the site ranking for Diptera in pitfalls was 5-1-2-3-4 in May and 1-4-5-3-2 in August. Whether such changes represent true seasonal effects or erratic non-seasonal natural fluctuations, or are an artifact of a sampling process which clearly does not suffice for making accurate site species richness estimates in every taxon (and was not designed for that purpose), is unknown. Whatever the cause, findings such as these suggest that this particular form of ordinal RBA measure will not be useful for making comparisons across sites.

Table 4 compares site species richness as estimated from conventionally identified specimens against the corresponding estimates based on RTU. There is some correspondence in rankings despite, for some taxa, large discrepancies between taxonomist's species number estimates and the RTU numbers estimated by project personnel. For example, Collembola from the February samples were placed to 40 RTU but to 78

Table 4. Site rankings by RTU ("Basic" RBA) and by taxonomists' estimates of species number.

Site	RTU RANK ABCDE	SPECIES RANK ABCDE
Spiders (Feb)	13245	21345
Spiders (May)	31245	21245
Chilopoda	31244	21244
Diplopoda	13244	12344
Colembola (Feb)*	12345	12345
Thrips	51341	51332
Beetles*	12345	12345
Ants	42135	52134
Non-ant Hymenoptera (Feb)	12335	21353

* Taxa giving the same site ranking by RTU as by species count.

species. Non-ant Hymenoptera were placed to 65 RTU but to 113 species. Cranston and Hillman (1992) have previously shown that such errors are both taxon- and operative-sensitive, and hence are unstable.

Table 4 suffices to demonstrate that the site rankings may vary, even amongst disparate sites, when RTU is used in place of (presumably more accurate) taxonomists' counts of species. One question which this raises is whether the counts of RTU could be made more like counts of species by a more careful assignment of specimens to RTU. In other words, what is the most appropriate protocol for RTU "identification"? A related question is whether steps can or should be taken to minimise systematic errors in RTU. In our data the clearest example of such errors occurred in the ants, for which RTU number was systematically underestimated by one of us (JT) through a failure to distinguish congeneric species when present, but systematically overestimated through the assignment of different castes to different RTU. The net effect on RTU number was small for all sites except site A, but such a result clearly is sample-specific and not generalisable. These two sources of error would not have been eliminated by a slower or more careful assignment of specimens to RTU.

Discussion

For the most part our field study repeats or reinforces themes which are common in invertebrate field survey work, such as that different taxa occur in different relative or absolute abundances at different sites and that different trapping procedures address different subsets of the fauna. The following have direct implications for the design of methods in conservation assessment:

1. natural seasonal or erratic fluctuations place a lower limit on the absolute time necessary for reliable survey of invertebrate biodiversity;
2. any site survey sufficient to provide an accurate estimate of species number over a wide range of taxa would likely be extremely costly and time consuming and also destructive of the site, therefore the goal of an accurate overall species number estimate for a wide range of taxa generally is not attainable;
3. as regards invertebrate survey, the relationship between fieldwork and post-fieldwork is such that there is far greater potential for time and cost savings in post-fieldwork than in fieldwork;

4. the taxon composition of samples is highly dependent on sampling procedures, making it difficult to standardise results across surveys;
5. site species richness rankings vary widely amongst taxa, and therefore are largely determined by sampling protocol or by the choice of which taxonomic groups to assess;
6. a naive "Ordinal RBA" signal based on a mix of insect orders and families, with class or phylum-level identification of other arthropods, is uninformative of site diversity for sites such as those we surveyed;
7. "Basic RBA" may produce site richness rankings inconsistent with the underlying species counts.

In addition, our observations on the meanings of "Rapid" and on the usefulness of species richness data in a conservation decision context suggest the need for a reappraisal of Rapid Biodiversity Assessment as that term currently is understood. Progress toward a meaningful set of biodiversity assessment protocols is unlikely unless (a) the present conflict over meanings of "Rapid" is resolved, and (b) the concept of "Biodiversity" is widened to include more than a mere species count.

It is significant that by its very nature an RTU count can never indicate which taxa deserve or require more conservation action than others. RTU-based methods cannot discriminate between common and rare taxa, between introduced and endemic taxa, or between those taxa which are threatened and those which are not. Taxon-based methods, in contrast, do preserve access to this type of information when it is available. The species-level identification phase of our study enabled us to make observations such as

1. The apparently greater species richness of Collembola at site A compared with site B all but vanishes if introduced species are ignored.
2. Species new to science were taken at a greater rate at sites A and B than at the other sites. (Site A yielded three new species of beetle and one collembolan; site B one beetle, one thrips and two wasps; site C one spider; site E one dipteran.)
3. Sites A, C and E produced significant range extensions to known genera or species. (Site A, a beetle of a genus known from New Zealand and an IUCN listed snail; Site C, ants of a genus known from mainland Australia; Site E, an IUCN listed, Australian endemic dragonfly known from only five sites.)

Information such as this is relevant to site management and conservation decisions. Such data always will be incomplete but it would be perverse to ignore that which can be obtained. RTU-based methods fail to retain the possibility of accessing this type of data, while a species count as an assay for biodiversity assigns it no value. Taxon-based identification facilitates the use of information other than the raw species number.

Conclusions

The term "Rapid Biodiversity Assessment", as currently used in, e.g., the draft National Strategy for the Conservation of Australia's Biological Diversity (DEST, 1995), blends several meanings of Rapid and a restricted meaning of Diversity into a hybrid concept. Evaluation of this hybrid requires that the parts be separated and individually assessed. We have addressed a few issues in RBA, some more adequately than others, and have sufficient evidence to demonstrate that a thorough reappraisal of RBA in invertebrate conservation decision making would be in order.

One major aspect which our study failed to examine but which warrants a detailed evaluation, is the potential of conventional identification using existing keys as an alternative to the RTU stage in a rapid (sense 1) assessment. Conventional identification by non-taxonomists likely would be slower than RTU assignment and less accurate than identification by experts. However, it would eliminate the need for separate voucher-specimen systems (essential when allocating large numbers of specimens to RTU) and avoid the systematic bias which comes from inappropriate definition of RTU units while also eliminating the resource bottleneck involved in identification by expert taxonomists. While this method might yield species number estimates no more accurate than those obtainable from RTU counts, the possibility of recovering information on the rarity, endemism, etc. of species also would be conserved.

Key-based conventional identification could well outperform both (i) RTU with calibration and confirmation by experts, and (ii) the direct expert identification of samples to species level, if evaluated on either an information-per-unit-time or information-per-unit-cost basis.

References

- Beattie, A.J., Majer, J.D. and Oliver, I., 1993. Rapid biodiversity assessment: a review. Pp. 4–14 in: *Rapid Biodiversity Assessment: proceedings of the biodiversity assessment workshop Macquarie University 1993*. Research Unit for Biodiversity and Bioresources, School of Biological Sciences, Macquarie University, Sydney.
- Coddington, J.A., Griswold, C.E., Silva Dávila, D., Peñaranda, E. and Larcher, S.F., 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pp. 44–60 in: Dudley, E.C. (ed), *The unity of evolutionary biology: proceedings of the fourth international congress of systematic and evolutionary biology*. Dioscorides Press: Portland.
- Conservation International, 1991. *A biological assessment of the Alto Madidi region and adjacent areas of northwest Bolivia*. Conservation International: Washington, DC.
- Cranston, P.S. and Hillman, T., 1992. Rapid assessment of biodiversity using 'biological diversity technicians'. *Australian Biologist* 5: 144–154.
- DEST (Federal Department of the Environment, Sports and Territories), 1995. *A National Strategy for the Conservation of Australia's Biological Diversity. Draft*. DEST: Canberra.
- Greenslade, P., and Greenslade, P.J.M., 1971. The use of baits and preservatives in pitfall traps. *Journal of the Australian Entomological Society* 10: 253–260.
- Heltsche, J.F. and Forrester, N.E., 1983. Estimating species richness using the jackknife procedure. *Biometrics* 39: 1–11.
- Trueman, J.W.H. and Cranston, P.S., 1994. *An evaluation of some methods of rapid biodiversity assessment for estimating arthropod diversity*. Report to the Department of the Environment, Sport and Territories. 66 pp. Unpublished.
- United Nations, 1993. *Rio Declaration on Environment and Development. UN Conference on Environment and Development, 1992, Rio de Janeiro, Brazil*. UN Department of Public Information: New York.

MEASURING INVERTEBRATE BIODIVERSITY: SURROGATES OF ANT SPECIES RICHNESS IN THE AUSTRALIAN SEASONAL TROPICS

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Abstract

Andersen, A.N., 1997. Measuring invertebrate biodiversity: surrogates of ant species richness in the Australian seasonal tropics. *Memoirs of the Museum of Victoria* 56(2): 355–359.

The search for surrogate measures of total species richness has taken two paths, one considering the number of higher-level taxa such as genera or families, and the other considering species richness within particular target taxa. A previous analysis of Australian ant faunas indicated that genus richness was often an unreliable predictor of species richness, and that the richness of particular target genera might be a better surrogate. The data presented here from the Kakadu region of the Northern Territory support this analysis. Correlations between site species and genus richness gave r-squared values of 0.37 at natural sites ($n = 22$) and 0.66 at disturbed sites ($n = 17$). In both cases, correlations with the richness of individual target genera (the eight richest genera, contributing 110 of the 163 species recorded) gave equivalent or higher r-squared values — up to 0.46 for *Melophorus* at natural sites, and 0.66 for *Melophorus* at disturbed sites. Stepwise linear regression using all target genera gave r-squared values of 0.92 at natural sites (with six of the eight genera contributing to the model), and 0.89 at disturbed sites (with only *Melophorus* and *Polyrhachis* contributing to the model). The effort required to obtain data on the richness of target genera is likely to be similar to that required for genus richness, making target genera a more attractive option for biodiversity surrogacy. The choice of target genera varies with the spatial scale (regional or national) of analysis, and diversity relationships among sites representing variation between habitats are not the same as those among sites representing variation in disturbance.

Introduction

There is an increasing demand for robust ecological indicators (McKenzie et al., 1995) for use in environmental assessment and monitoring programs. Such indicators are most commonly required in the context of monitoring for ecological change following habitat disturbance (Noss, 1990; Spellerberg 1993), and invertebrates have often been targeted for such use (James and Evison, 1979; Greenslade and Greenslade, 1984; Disney, 1986; Rosenberg et al., 1986; Majer, 1989; Andersen, 1990; Williams, 1993).

More recent attention has focussed on the development of indicators of biodiversity *per se*, particularly in relation to estimates of species richness in highly diverse groups, such as invertebrates, where comprehensive species-level surveys are usually not an option (Hammond, 1994; Oliver and Beattie, 1996). The search for surrogates of total species richness has taken two paths, one considering the number of higher-level taxa (genera, families, etc.; Gaston and Williams, 1993; Prance, 1994; Williams and Gaston, 1994), and the other considering species

richness within particular target taxa (Kremen, 1994; Pearson, 1994; Oliver and Beattie, 1996).

In a previous analysis of Australian ant faunas (Andersen, 1995a), I showed that genus richness has limited reliability as a surrogate of species richness. Genus and species richness were closely related within a particular region, but the relationship showed large biogeographic variation, and was confounded by sampling area and sampling intensity. On a continental scale, the richness of particular target genera was more highly correlated with total species richness than was genus richness.

Here, I further explore indicators of species richness in Australian ant faunas by comparing higher-taxon richness with the richness of target genera as surrogates within a particular region. When searching for indicator taxa in the context of ecological change, it is important to differentiate between change across habitats or other aspects of the biophysical environment on the one hand, and ecological change within a particular environment due to disturbance on the other. Taxa providing a good indication of vari-

ation between habitats do not necessarily provide a good indication of the effects of disturbance within a habitat, and *vice versa*. Similarly, the best surrogate of between-habitat variation in diversity may not be the best surrogate for indicating changes within a particular habitat due to disturbance. This paper also explores the effects of disturbance on diversity patterns and the reliability of surrogates.

Methods

Study Sites

The study was conducted in and around Kakadu National Park, approximately 250 km E of Darwin in the seasonal tropics of northern Australia. Mean annual rainfall in the region is approximately 1400 mm, almost all of which falls between November and April (see Taylor and Dunlop, 1985). Temperatures are constantly high, ranging from overnight minima of about 15°C during July to daytime maxima of about 40°C during October. Soils are predominantly infertile, sandy clay loams, supporting savanna woodlands and open forests dominated by species of *Eucalyptus* (Mott et al., 1985; Taylor and Dunlop, 1985). The study was restricted to these savanna vegetation types, and did not include other regional habitats such as floodplains and monsoon rainforest.

A total of 39 sites were selected for study, comprising 22 'natural' sites that had been relatively undisturbed by human activity, and 17 disturbed sites. The natural sites were widely dispersed (separated by up to 100 km from each other), and chosen to represent the full range of savanna types in the region. The 17 disturbed sites were all located within approximately 25 km², inside the Ranger Uranium Mine lease near Jabiru, and were selected to represent a range of disturbance levels within a relatively small area. Ten of these were located adjacent to the immediate minesite, and represented a range of disturbance histories indirectly associated with mining activity. The level of disturbance ranged from slight (e.g., a roadside strip with intact vegetation, but subject to edge effects) to severe (vegetation completely cleared, with unmanaged regrowth). The remaining seven sites were located on the mine's northern waste rock stockpile (Unger and Milnes, 1992), and represented a range of stages of revegetation.

Sampling

Local ant diversity is exceptionally high in the region, with up to 100 or more species occurring per hectare (Andersen, 1992; Andersen and

Patel, 1994). Most of these are uncommon, such that a comprehensive census of species at a single site requires a prolonged period of high sampling intensity. This is obviously not a feasible option within the context of normal biological survey programmes. The sampling intensity used here was designed to be achievable within the resources of normal survey programmes, with the aim of providing comparative, rather than comprehensive, data on site species richness.

Ants were sampled primarily using pitfall traps (4 cm diameter plastic specimen jars, partly filled with ethanol as a preservative), which have been widely used in quantitative studies of Australian ant communities (Andersen, 1995b), and have been shown to provide a reliable estimate of species composition in the Kakadu region (Andersen, 1991). A 5 by 3 trapping grid with 10 m spacing was established at each site, and traps were operated for a 48 hr period at each site during July and November 1992, and November 1993. Trapping was supplemented by opportunistic, daytime handcollections.

Analysis

Ants were sorted to species, and samples from different time periods were combined to produce a single species list for each site, from which numbers of species and genera were counted. The eight richest of the 32 genera recorded were selected for target taxa analysis: *Monomorium* (21 species), *Pheidole* (16), *Melophorus* (15), *Iridomyrmex* (14), *Rhytidoponera* (13), *Meranoplus* (13), *Camponotus* (11) and *Polyrhachis* (7). Together these genera contributed 110 (67%) of the total of 163 species (see Andersen et al., 1996 for details of species composition).

Pearson correlation coefficients were calculated for the relationships between total ant species richness and (a) genus richness, and (b) richness of each of the selected target genera, considering natural and disturbed sites separately. The relationship between total species richness and combinations of the richnesses of target genera was then analysed by stepwise linear regression, using STATISTIX 4.1, again considering natural and disturbed sites separately.

Results

Diversity patterns varied markedly between natural and disturbed sites. At natural sites, genus richness was rather poorly correlated ($r^2 = 0.37$; Fig. 1) with species richness, and was

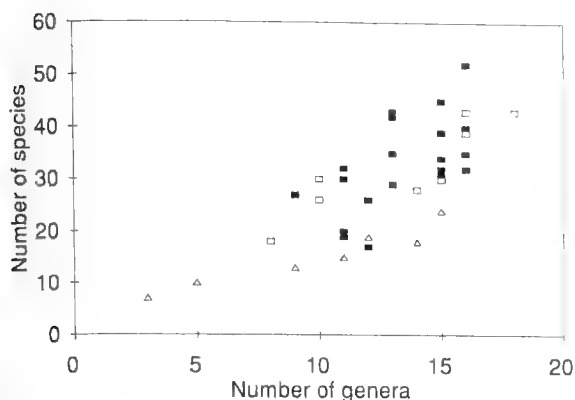


Figure 1 Relationship between number of ant species and number of ant genera at natural sites (closed squares; $r^2 = 0.366$, $p < 0.001$, $n = 22$) and disturbed sites (open triangles (waste-rock sites) and open squares (other disturbed sites); $r^2 = 0.655$, $p < 0.001$, $n = 17$) in the Kakadu region.

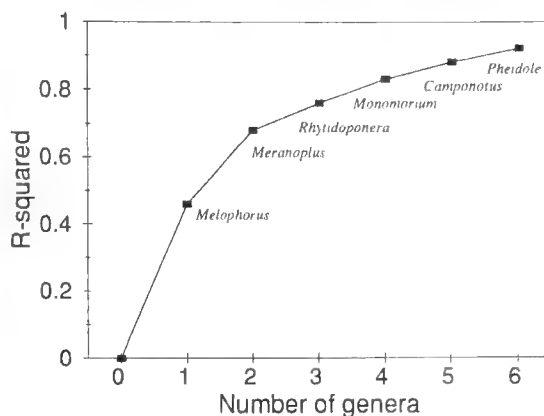


Figure 2 Relationship between number of ant species and numbers of species of selected ant genera, based on results of stepwise linear regression. The curve shows the increase in the correlation coefficient (r -squared) as additional genera are introduced into the regression.

therefore not a reliable surrogate. The richness of the best target genus (*Melophorus*, $r^2 = 0.46$; Table 1) provided a better indication of total species richness. The inclusion of a second genus (*Meranoplus*) improved the relationship substantially ($r^2 = 0.68$), with the final step-wise linear regression model (including six of the eight richest genera) accounting for 92% of the variation in total species richness (Fig. 2).

At disturbed sites, species richness showed continuous variation from the least revegetated waste-rock sites to the least impacted sites (Fig. 1). Overall, genus richness provided a good indication ($r^2 = 0.66$) of total species richness, with the relationship being particularly strong

($r^2 = 0.91$) at waste-rock sites. The richness of the best target genus (again *Melophorus*, $r^2 = 0.66$; Table 1) also provided a good indication of total species richness at disturbed sites. The final step-wise linear regression model included only *Melophorus* and *Polyrhachis*, and accounted for 89% of the variation in total species richness.

Discussion

Comparisons between potential surrogates obviously need to take into account the effort required to measure them. The effort required to sample and discriminate species from a site varies markedly with genus. The task is obviously far easier for genera containing large and conspicuous species (e.g., *Camponotus*, *Rhytidoponera* and *Polyrhachis*) than it is for genera containing numerous small, inconspicuous and morphologically similar species (e.g., *Monomorium*). The effort required to sample a genus like *Melophorus* lies somewhere inbetween, and is probably comparable to the effort required to measure genus richness.

Given these observations on sampling effort, the richness of target genera appears to be more useful than genus richness as a surrogate of total species richness in Australian ant faunas. This is especially true when considering different habitats, but less so for disturbance-related changes within a particular habitat.

The choice of target genera will vary substantially. When considering different habitats, an appropriate target genus for continental-scale comparisons may not be appropriate for analy-

Table 1. Correlations between total number of ant species and number of species of selected ant genera. Data are r -squared values, with statistical significance indicated as follows: ns not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	Natural sites	Disturbed sites
<i>Rhytidoponera</i>	0.382***	0.620***
<i>Meranoplus</i>	0.401***	0.391**
<i>Monomorium</i>	0.339**	0.606***
<i>Pheidole</i>	0.260**	0.455**
<i>Iridomyrmex</i>	0.169*	0.337**
<i>Camponotus</i>	0.073 ^{ns}	0.339**
<i>Melophorus</i>	0.464***	0.661***
<i>Polyrhachis</i>	0.134*	0.419**

ses confined to a particular region. For example, *Camponotus* appears to be an excellent target genus for comparing sites distributed throughout Australia ($r^2 = 0.83$, $n = 10$; Andersen, 1995a), but was ineffective at the natural sites described here ($r^2 = 0.07$). Further, just as genus-species relationships varied between natural and disturbed sites, so did both the reliability and composition of the optimum set of genera for target-taxa analysis.

In addition to identifying potential surrogates of ant species richness, this study has shown that disturbance and biophysical variation have different effects on species packing. This points to the need for distinguishing between different types of ecological change when searching for ecological indicators.

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References

- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–357.
- Andersen, A.N., 1991. Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. *Australian Journal of Ecology* 16: 273–279.
- Andersen, A.N., 1992. Regulation of 'momentary' diversity by dominant species in exceptionally rich ant communities of tropical Australia. *American Naturalist* 140: 401–420.
- Andersen, A.N., 1995a. Measuring more of biodiversity: genus richness as a surrogate of species richness in Australian ant faunas. *Biological Conservation* 73: 39–43.
- Andersen, A.N., 1995b. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in terms of stress and disturbance. *Journal of Biogeography* 22: 15–29.
- Andersen, A.N., Morrison, S. and Belbin, L., 1996. *The role of ants in minesite restoration in the Alligator Rivers Region of the Northern Territory*. Unpublished report to the Environmental Research Institute of the Supervising Scientist, CSIRO Division of Wildlife and Ecology: Darwin.
- Andersen, A.N. and Patel, A.D., 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on foraging success and forager abundance of other species. *Oecologia* 98: 15–24.
- Disney, R.H.L., 1986. Assessments using invertebrates: posing the problem. Pp. 271–293 in: Usher, M.B. (ed), *Wildlife conservation evaluation*. Chapman and Hall: London.
- Gaston, K.J. and Williams, P.H., 1993. Mapping the world's biodiversity — the higher taxon approach. *Biodiversity Letters* 1: 2–8.
- Greenslade, P.J.M. and Greenslade, P., 1984. Invertebrates and environmental assessment. *Environment and Planning* 3: 13–15.
- Hammond, P.M., 1994. Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London, Series B* 345: 119–136.
- James, A. and Evison, L., (eds), 1979. *Biological indicators of water quality*. John Wiley: Chichester.
- Kremen, C., 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecological Applications* 4: 407–422.
- McKenzie, D.H., Hyatt, D.E. and McDonald, V.J., 1995. *Ecological indicators, Vols I and II*. Elsevier: London.
- Majer, J.D. (ed.), 1989. *Animals in primary succession — the role of fauna in reclaimed lands*. Cambridge University Press: Cambridge.
- Mott, J.J., Williams, L., Andrew, M.H. and Gillison, A.N., 1985. Australian savanna ecosystems. Pp. 56–82 in: Tothill, J.C. and Mott, J.J. (eds), *Ecology and management of the world's savannas*. Australian Academy of Science: Canberra.
- Noss, R.N., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4: 355–364.
- Oliver, I. and Beattie, A.J., 1996. Designing a cost-effective invertebrate survey: a test of some methods for the rapid assessment of invertebrate biodiversity. *Ecological Applications* 6: 594–607.
- Pearson, D.L., 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society of London, Series B* 345: 75–79.
- Prance, G.T., 1994. A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. *Philosophical Transactions of the Royal Society of London, Series B* 345: 89–99.
- Rosenberg, D.M., Danks, H.V. and Lehmkuhl, D.M., 1986. Importance of insects in environmental impact assessment. *Environmental Management* 10: 773–783.
- Spellerberg, I.F., 1993. *Monitoring ecological change*. Cambridge University Press: London.
- Taylor, J.A. and Dunlop, C., 1985. Plant communities of the wet-dry tropics of Australia: the Alligator

- Rivers region, Northern Territory. *Proceedings of the Ecological Society of Australia* 13: 83–128.
- Unger, C.J. and Milnes, A.R., 1992. Rehabilitation at Ranger Uranium Mines. Pp. 221–231 in: Moffatt, I. and Webb, A. (eds), *Conservation and development issues in northern Australia*. North Australian Research Unit: Darwin.
- Williams, K.S., 1993. Use of terrestrial arthropods to evaluate restored riparian woodlands. *Restoration Ecology* 1: 107–116.
- Williams, P.H. and Gaston, K.J., 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation* 67: 211–217.

INTERPRETING DATA FROM PITFALL-TRAP SURVEYS: CRICKETS AND SLUGS IN EXOTIC AND NATIVE GRASSLANDS OF THE AUSTRALIAN CAPITAL TERRITORY

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Abstract

Melbourne, B.A., Gullan, P.J. and Su, Y.N., 1997. Interpreting data from pitfall-trap surveys: crickets and slugs in exotic and native grasslands of the Australian Capital Territory. *Memoirs of the Museum of Victoria* 56(2): 361–367.

We use data from a pitfall-trap survey of 23 grassland sites to examine the effect of grassland type on the abundance of crickets and slugs and to demonstrate the problems associated with interpreting data obtained by pitfall-trapping. The data presented here are for four species of native cricket (Insecta: Orthoptera: Gryllidae: *Bobilla victoriae* Otte and Alexander, *Teleogryllus commodus* (Walker), *Buangina anemba* Otte and Alexander, *Pteronemobius arima* Otte and Alexander) and five species of introduced slug (Gastropoda: Pulmonata: Limacidae: *Deroceras reticulatum* (Müller), *Lehmannia* (*Lehmannia*) *nyctelia* (Bourguignat), *Limax maximus* Linnaeus; Milacidae: *Milax gagates* (Draparnaud); Arionidae: *Arion intermedius* Normand). The survey included three types of native grassland (*Themeda*, *Stipa*, *Danthonia*), two types of exotic grassland (*Phalaris*, *Avena*), and two seasons (summer, autumn). In addition to the survey, the effect of habitat structure on the efficiency of pitfall traps was examined in a well-replicated field experiment. The experiment was carried out in *Themeda* grassland, which was manipulated to create three levels of habitat structure. Habitat structure was found to affect pitfall-trap efficiency for crickets but not for slugs. We show that it is necessary to use knowledge of the effect of habitat structure on pitfall-trap efficiency for different species to allow confident interpretation of data from field surveys. Grassland type had a significant effect on the abundance of both crickets and slugs. *Bobilla victoriae* and *T. commodus* were both found to have high abundances in *Phalaris*, an improved pasture. Slugs appear to be highly invasive of native grasslands.

Introduction

Pitfall trapping is one of the most widely used and effective methods for sampling populations and communities of small, surface-active arthropods. The method is inexpensive, requires minimal field time and generates a large amount of data, such that many replicates can be acquired with much less effort than other methods available for sampling ground-dwelling species. As a result, it is becoming an increasingly popular method for biodiversity surveys. However, data obtained by pitfall trapping are subject to several potential sources of error, which include differences in susceptibility between sexes, life stages and species, and spatial or temporal variation in trap efficiency (Greenslade, 1964; Luff, 1975; Southwood, 1978; Halsall and Wratten, 1988; Topping, 1993).

One serious potential source of error that has received little attention is the effect of the physical structure of the habitat on pitfall-trap efficiency. For example, Greenslade (1964)

examined the effect of habitat structure on pitfall-trap efficiency in grasslands and found that pitfall-trap catches were adversely affected in dense grass but his experiment had little replication. Several authors have noted that speed of animal movement is an important determinant of pitfall-trap catches (Greenslade, 1973; Andersen, 1983; Morrill et al., 1990). Thus, for many arthropod species lower pitfall-trap catches might be expected in dense habitats compared to open habitats because speed of animal movement is decreased due to either lower penetrability (Greenslade, 1964) or lower temperatures (Topping and Sunderland, 1992). However, dense habitats are not expected to adversely affect the efficiency of pitfall-traps for all species. Halsall and Wratten (1988) for example, found that speed of movement did not affect capture efficiency for some carabid species and Topping (1993) suggested that positive effects of dense vegetation on pitfall-trap catches could be expected for some spiders. Also, temperature will not always be lower in dense habitats than in open habitats and the

reverse situation will be encountered depending on time of day and season (Geiger, 1965). Thus, effects on pitfall-trap efficiency due to temperature will depend on the diurnal and seasonal timing of activity for a given species. In summary, habitat structure is expected to affect pitfall-trap efficiency for different species in different ways.

Studies in which the fauna of habitats with different physical structure are compared are common in agricultural and ecological investigations and are likely to be the most common case for biodiversity surveys. For such studies, it is important to establish the effects of habitat structure on pitfall-trap efficiency to ensure that results are not confounded by differences in trapping efficiency. In this paper we use pitfall traps to examine the effect of grassland type on the abundance of crickets and slugs in five types of grassland that occur near Canberra, Australia. The physical structure of the grassland types that we surveyed encompassed a range from very dense to very open. In addition to the grassland survey, we conducted an experiment in which habitat structure was manipulated to determine the effect of habitat density on pitfall-trap efficiency for different species. We illustrate the way knowledge of a species' response to habitat structure can be used to aid interpretation of data from field surveys.

Methods

Pitfall traps

Pitfall traps were similar to the design used by Margules (1993). Each trap consisted of a plastic cup, 9 cm in diameter and 12 cm deep, with gently sloping sides. The cup was inserted into a polyvinyl chloride (PVC) sleeve, 9 cm in diameter and 14 cm deep, set flush with the soil surface. The PVC sleeves were installed using a soil auger of slightly smaller diameter such that very little disturbance was made to the area surrounding the trap. A 60 cm long, 7 cm high galvanised iron drift fence was positioned across the centre line of the cup and secured at each end by a 15 cm rod driven into the ground. Drift fences have been shown to increase the number of organisms caught by creating a larger area of interception (Morrill et al., 1990). A 20 cm by 20 cm galvanised iron roof was positioned over the cup, flush with the drift fence, and secured by four legs, 20 cm in length, driven into the ground. The trap design was particularly robust to disturbance by grazing animals. Preservative fluid (ethylene glycol in various concentrations,

see below) was added to the cup to a depth of 4 cm (125 ml) and a few drops of Teepol detergent were added to reduce the surface tension.

Grassland survey

The study area was located in the northern half of the Australian Capital Territory (ACT) and encompassed an area of approximately 450 km (Fig. 1). Grassland sites were generally in valley bottoms or on gentle slopes associated with creek catchments and river corridors, in lowland treeless areas at altitudes between 550 m and 650 m. The survey design (Fig. 1) included 23 sites from five broadly classified grassland types, which were stratified into seven regions to ensure that differences arising between grassland types were not confounded

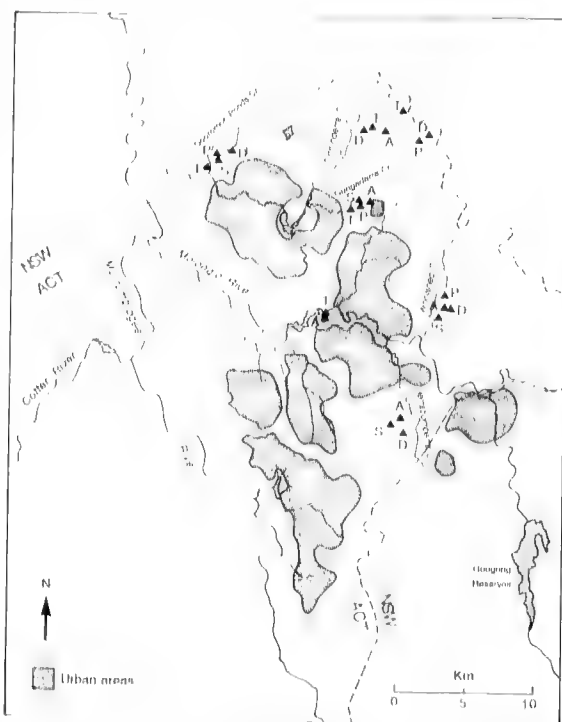


Figure 1. The study area and locations of the grassland survey sites. The survey design consisted of five grassland types stratified into seven regions. Most of the regions were defined by catchment areas. The major rivers and creeks are shown. Three types of native grassland (*Themeda* (T), *Danthonia* (D), *Stipa* (S)) and two types of exotic grassland (*Phalaris* (P), *Avena* (A)) were included in the survey.

with differences between regions (Hurlbert, 1984). Six of the geographical regions were water catchments and the seventh encompassed Mulligan's Flat Nature Reserve. Full details of site locations are given in Melbourne (1993).

The five grassland types included three native grassland types and two exotic grassland types. Grassland types were classified subjectively. The native grasslands corresponded roughly to three native grassland communities of the Southern Tablelands recognised by Benson (1994). The five grassland types had the following general characteristics:

1. *Themeda* grassland: dense *Themeda triandra* with an herbaceous stratum that included thick litter and senescent plant material to a depth of about 20 cm. Introduced species recorded at these sites included *Cirsium vulgare*, *Hypochoeris radicata*, *Paspalum dilatatum* and *Phalaris aquatica* but these were never conspicuous and mostly consisted of isolated individuals. Similar to "Community 2" of Benson (1994).
2. *Stipa* grassland: dominated by *Stipa* spp. (typically *Stipa bigeniculata*) often with a minor component of *Danthonia* spp. The structure was dominated by *Stipa* spp., which tends to form tussocks 20 cm to 30 cm in height with relatively open inter-tussock spaces. Many exotic species also were recorded including *Bromus hordeaceus*, *Carthamus lanatus*, *Hypochoeris radicata*, *Phalaris aquatica*, *Plantago lanceolata*, *Trifolium* spp. and *Vulpia bromoides*. Similar to "Community 5" of Benson (1994).
3. *Danthonia* grassland: dominated by *Danthonia* spp. (typically *Danthonia carphoides* and *Danthonia* sp.) often with scattered tussocks of *Stipa bigeniculata*, *Themeda triandra* or *Bothriochloa macra*. Generally, the structure was relatively open with some bare ground. These grasslands were short, with small tussocks of *Danthonia* spp. to a height of 15 cm. Many exotic species also were recorded including *Aira elegans*, *Briza minor*, *Hypochoeris radicata*, *Panicum effusum* and *Trifolium* spp. Similar to "Community 1" of Benson (1994).
4. *Phalaris* grassland: improved pasture dominated by *Phalaris aquatica*. The herbaceous stratum was to a height of 20 cm to 30 cm. The stands were relatively pure but with some *Trifolium* spp. and turf. Other exotic species recorded included *Cirsium vulgare* and *Hypochoeris radicata*. At the time of sampling in summer the structure was relatively

even and dense but with no tussocks. At the time of sampling in autumn these grasslands had been lightly grazed by cows, sheep or horses and the structure had changed to consist of small tussocks with inter-tussock spaces that had been grazed to ground level.

5. *Avena* grasslands: *Avena fatua* present as a major component but the sites also included a large number of weedy grasses and other exotic species including *Bromus* spp., *Carthamus lanatus*, *Cirsium vulgare*, *Cynodon dactylon*, *Echium plantagineum*, *Hypericum perforatum*, *Hypochoeris radicata*, *Paspalum dilatatum*, *Phalaris aquatica*, *Plantago lanceolata*, *Rumex acetosella*, *Salvia verbenaca*, *Sisymbrium officinale*, *Trifolium* spp. and *Vulpia bromoides*.

The relative density of the different grassland types, from most dense to least dense, was ranked as follows: (summer) *Themeda* > *Phalaris* > *Avena* = *Stipa* > *Danthonia*; (autumn) *Themeda* > *Stipa* > *Avena* = *Phalaris* > *Danthonia*.

Eight traps were installed at each site in a grid, such that the minimum distance between two traps was 10 m. In smaller sites, the trapping area was situated in the centre of the site while in larger sites the trapping area was situated at least 50 m from the edge of the grassland. The alignments of drift fences were randomised on four compass points (0°, 45°, 90°, 135°), with each compass point replicated twice at each site. Traps were operated for a two week period in summer (24 January 1993 to 7 February 1993) and a six week period in autumn (22 April 1993 to 3 June 1993). After installation, traps remained closed for at least one week and up to three weeks before being opened for the summer sample. The PVC sleeves remained installed but the holes were covered between trapping periods. Preservative fluid consisted of either 50% (summer) or 80% (autumn) ethylene glycol with water. The samples were sorted 'blind' to avoid unintentional biases in sorting effort between grassland sites. Representative samples of crickets were identified by D.C.F. Rentz and of slugs by B.J. Smith. Voucher specimens of crickets will be deposited in the Australian National Insect Collection, CSIRO, Canberra, and B.J. Smith (Queen Victoria Museum, Launceston, Tasmania) has retained voucher specimens of the slugs. Counts of the number of individuals of each taxon caught in the eight pitfall traps were summed to produce a single value for each site.

Since the sampling design was unbalanced and included both fixed and random effects, residual maximum likelihood (REML) methods (Engel, 1990) were used for the statistical analysis, treating *grassland type* as a fixed effect and *region* as a random (block) effect. The data for all taxa were log-transformed to remedy heteroscedasticity, which was evident from plots of standardised residuals versus fitted values. The modelling procedure was as follows. First, the factors *grassland type* and *region* were fitted to produce a maximal model. This model was used to predict means for the number of individuals caught in each grassland type. Second, to test for an effect of grassland type, a sub-model consisting of the 'constant' parameter was fitted and the associated change in deviance was determined. Grassland type was considered significant if the change in deviance exceeded the χ^2 value for the appropriate degrees of freedom at the $P = 0.05$ level.

Pitfall-trap experiment

The study site was located within a 20 hectare contiguous area of *Themeda triandra* grassland near the *Themeda* survey site in the Gungaharra Creek catchment (see Fig. 1 35°12'40"E, 149°06'50"S). The study area was a uniform area of grassland, 60 m by 50 m, divided into thirty 10 m by 10 m plots. The experimental design included three types of plots, in two of which the density of the habitat immediately surrounding the pitfall traps was manipulated. Two pitfall traps were installed 2.5 m apart at the centre of each 10 m by 10 m plot. In the first type of plot (*unmodified*) no modification was made to the density of the vegetation. In the second type of plot (*cleared*) all vegetation (living and dead) was removed from within an 80 cm radius of each pitfall trap. In the third type of plot (*litter removed*) only litter and senescent plant material was removed from within an 80 cm radius of each pitfall trap. This manipulation created inter-tussock spaces such that the density of the habitat was intermediate between the *cleared* and *unmodified* plots. The three types of plots were arranged in a randomised block design with ten replicates for each treatment (habitat density) and with treatments randomly assigned to plots within blocks. We attempted to minimise disturbance effects by leaving a ten day period between the habitat manipulations and the commencement of trapping. This period was a trade-off between allowing initial disturbance effects, such as nest disruption, to dissipate and to minimise delayed effects, such as immi-

gration of new species into the cleared and litter removed plots. Traps were operated for two weeks in autumn (5 April 1993 to 20 April 1993). A 50% solution of ethylene glycol was used as the preservative fluid. The alignments of drift fences were randomised on four compass points as described previously.

Analysis of variance was used to test for the significance of the factor *habitat density*. Data from the two pitfall traps in each plot were summed and made up one replicate. The factor *block* was included in the analysis of variance model as a blocking factor. To test for differences between means, a least significant difference (LSD) was calculated from: $t \times \text{s.e.d.}$, where s.e.d. = standard error of the differences of means. Plots of the standardised residuals versus fitted values, and standardised residuals versus expected normal quantiles were inspected. The untransformed data were found to satisfy assumptions of normality and constant variance.

Results

Four species of cricket and five species of slug were captured in the grassland survey. The crickets all were from the family Gryllidae and are all native to Australia. Cricket species caught (total captures in brackets) were *Bobilla victoriae* Otte and Alexander (8325), *Teleogryllus commodus* (Walker) (650), *Buangina anemba* Otte and Alexander (25) and *Pteronemobius arima* Otte and Alexander (4). There was a significant effect of grassland type on the abundance of *B. victoriae* and *T. commodus* for summer and *T. commodus* for autumn (Fig. 2). The pattern of relative catch sizes between different grassland types was similar for summer and autumn in both species (Fig. 2). The catch size of *B. victoriae* was highest in *Phalaris* grassland and approximately equal in all other grassland types, while the catch size of *T. commodus* was lower in *Danthonia* and *Avena* grassland in comparison to the other grassland types (Fig. 2). *B. anemba* was caught in all grassland types except *Stipa*. The few individuals of *P. arima* were recorded from *Themeda*, *Stipa* and *Avena* grasslands.

A total of 3012 slugs were caught in the grassland survey. The slug species caught were *Dero-ceras reticulatum* (Müller) (Limacidae), *Lehmannia (Lehmannia) nyctelia* (Bourguignat) (Limacidae), *Limax maximus* Linnaeus (Limacidae), *Milax gagates* (Draparnaud) (Milacidae) and *Arion intermedius* Normand (Arionidae). All species have been introduced to Australia

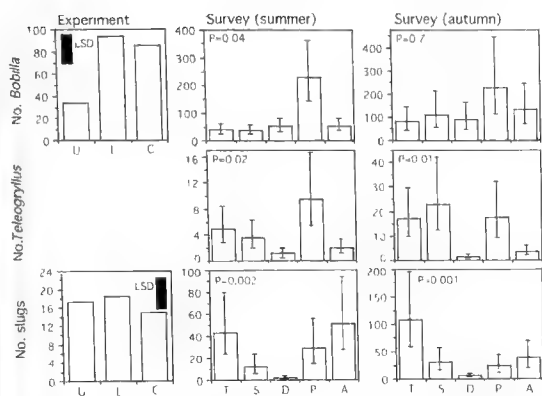


Figure 2. Comparison of pitfall-trap catch sizes of crickets and slugs in response to experimental manipulation of habitat structure and to grassland type. Results from the experiment show mean pitfall-trap catch sizes per plot estimated using ANOVA. U = unmodified, L = litter removed, C = cleared. LSD stands for least significant difference, which is equal to approximately two times the standard error of the differences of means. Comparison of means using the LSD indicates the significance of differences between means at $P = 0.05$. The survey results show means, estimated using REML models, for the number of individuals of crickets and slugs caught per site in pitfall-traps. P values indicate the level of significance for the factor grassland type. Bars indicate standard errors. T = *Themeda*, D = *Danthonia*, S = *Stipa*, P = *Phalaris*, A = *Avena*. The relative density of grassland types and experimental treatments, from most dense to least dense, was ranked as follows: T > P > A = S > D (summer); T > S > A = P > D (autumn); U > L > C.

since European settlement. The number of slugs of each species was not scored but an inspection of 43 traps indicated that about 90% of all individuals were Limacidae. There was a significant effect of grassland type on the catch size of slugs in both seasons (Fig. 2). The pattern of relative catch sizes between the native grassland types was the same for summer and autumn with catch sizes being highest in *Themeda*, lowest in *Danthonia* and intermediate in *Stipa* (Fig. 2). Catch sizes of slugs in *Phalaris* and *Avena* were approximately equal to catch sizes in *Themeda* for summer but were lower than in *Themeda* for autumn (Fig. 2).

In the pitfall-trap experiment, a total of 2137 specimens of *Bobilla victoriana* and 504 slugs (mostly Limacidae) were caught. There was a significant effect of the habitat density treatment for *B. victoriana* ($P < 0.001$) but not for slugs. Catches of *B. victoriana* were significantly lower in the dense habitat of the unmodified

plots compared to the litter removed and cleared plots, while catches of slugs were approximately equal at all habitat densities (Fig. 2).

Discussion

We begin this discussion by showing that it is necessary to use the results from the experiment to interpret the results from the survey of different grassland types. We found that, in general, the results from the experiment indicate that the survey results reflect true patterns in abundance for crickets and slugs. We conclude with some discussion on the ecological significance of these abundance patterns.

In the summer survey of different grassland types, pitfall-trap catches of *Bobilla victoriana* for summer were several times higher in *Phalaris* than in the other grassland types. The results from the experiment suggest that this result reflects a true elevated abundance in *Phalaris*, rather than an effect of habitat density on pitfall-trap efficiency. This is because pitfall-trap efficiency was shown to decline as the density of the habitat increased, yet the *Phalaris* grasslands were ranked second most dense at the time of sampling in summer. Indeed, for this reason, the abundance of *B. victoriana* in *Phalaris* relative to other grassland types is more likely to have been underestimated rather than overestimated (except in the case of *Themeda* grasslands). *Teleogryllus commodus* was not caught in the experiment, so we have no measure of its response to habitat structure. However, if we assume that it behaves in a similar way to *B. victoriana*, its pattern of abundance in the different grassland types also is unlikely to be due to an effect of habitat structure on pitfall-trap efficiency, since it was caught most in the dense grassland types and least in the more open grasslands.

For slugs, the results from the experiment indicate that pitfall-trap efficiency is not affected by habitat density. We can thus be confident that the observed pattern of slug catches in the different types of grassland was not due to an effect of habitat structure on pitfall-trap efficiency. In this case, the experimental results are very important to the interpretation of the survey results since the pattern of abundance for slugs among the different grassland types was congruent with the density ranking of the five grassland types for both seasons (more slugs were caught in dense grasslands). In the absence of the experimental results, an alternative hypothesis to explain the observed pattern is easy to formulate: fewer slugs were caught in

open areas because slugs moved less on the drier substrate, which reduced pitfall-trap efficiency.

The crickets captured in the survey were all native species (Otte and Alexander, 1983). Two species appear rare or rarely caught in this region. *Buangina anemba* is otherwise known from only two localities in eastern NSW (Penrith and Armidale) and there is only one previous record from the ACT of *Pteronemobius arima* (from 1951), which otherwise has a range that includes the northern Northern Territory and the eastern periphery of Queensland and New South Wales (Otte and Alexander, 1983). *Bobilla victoriae* was the most common species caught and its abundance was clearly several times higher in *Phalaris* than in the other grassland types. There appears to be no previously published information on the ecology of this species, other than to note that it is known from open grassy areas of the Great Dividing Range of NSW and Victoria (Otte and Alexander, 1983). *Teleogryllus commodus* also was high in abundance in *Phalaris*. This species is a known and sometimes serious pest of improved pasture in Australia and New Zealand (Browning, 1954; Blank and Olsen, 1981), including pasture sown to *Phalaris* (Browning, 1954). Its distribution and abundance appears to be related in part to moisture and availability of shelter from the sun, particularly in the form of cracks in the soil (Browning, 1954). Thus, the low abundance of *T. commodus* in *Danthonia* grasslands compared to other grassland types could be explained by the drier conditions and absence of shelter from the sun. Given that *B. victoriae* shows a clear preference for exotic pasture, we suggest that it may be a previously unrecorded pest, in addition to *T. commodus*, of improved pasture in the ACT region.

All of the slug species caught in the grassland survey were introduced species (van Regteren Altena and Smith, 1975; Smith and Kershaw, 1979; Smith 1992). Introduced slugs appear to be highly invasive of native grasslands, given the right environmental conditions, since their abundance in native grasslands, particularly *Themeda* and *Stipa*, is as high as in exotic grasslands.

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References

- Andersen, A.N., 1983. Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology* 8: 127–137.
- Benson, J.S., 1994. The native grasslands of the Monaro region: Southern Tablelands of NSW. *Cunninghamia* 3: 609–650.
- Blank, R.H. and Olsen, M.H., 1981. The damage potential of the black field cricket *Teleogryllus commodus*. *New Zealand Journal of Agricultural Research* 24: 251–258.
- Browning, T.O., 1954. Observations on the ecology of the Australian field cricket, *Gryllulus commodus* Walker in the field. *Australian Journal of Zoology* 2: 205–222.
- Engel, B., 1990. The analysis of unbalanced linear models with variance components. *Statistica Neerlandica* 44: 195–219.
- Geiger, R., 1965. *The climate near the ground*. 4th Edition. Harvard University Press: Cambridge, Massachusetts. 611 pp.
- Greenslade, P.J.M., 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* 33: 301–310.
- Greenslade, P.J.M., 1973. Sampling ants with pitfall traps: digging in effects. *Insects Sociiaux* 20: 343–353.
- Halsall, N.B. and Wratten, S.D., 1988. The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology* 13: 293–299.
- Hurlbert, S.A., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Luff, M.L., 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* 19: 345–357.
- Margules, C.R., 1993. The Wog Wog habitat fragmentation experiment. *Environmental Conservation* 19: 316–325.
- Melbourne, B.A., 1993. *The assessment of insect biodiversity. A case study: ants and carabid beetles in grasslands of the A.C.T.* Unpublished honours thesis. The Australian National University: Canberra. 100 pp.

- Morrill, W.L., Lester, D.G. and Wrona, A.E., 1990. Factors affecting the efficiency of pitfall traps for beetles (Coleoptera: Carabidae and Tenebrionidae). *Journal of Entomological Science* 25: 284-293.
- Otte, D. and Alexander, R.D., 1983. The Australian crickets (Orthoptera: Gryllidae). *Monograph of the Academy of Natural Sciences of Philadelphia* 22: 1-477.
- Smith, B.J., 1992. *Non-marine Mollusca*. W. W. K. Houston (ed.). *Zoological Catalogue of Australia*. Vol. 8. AGPS: Canberra. 405 pp.
- Smith, B.J. and Kershaw, R.C., 1979. *Field guide to the non-marine molluscs of south eastern Australia*. Australian National University Press: Canberra. 285 pp.
- Southwood, T.R.E., 1978. *Ecological methods*. Chapman and Hall: London. 524 pp.
- Topping, C.J., 1993. Behavioural responses of three linyphiid spiders to pitfall traps. *Entomologia Experimentalis et Applicata* 68: 287-293.
- Topping, C.J. and Sunderland, K.D., 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology* 29: 485-491.
- van Regteren Altena, C.O. and Smith, B.J., 1975. Notes on the introduced slugs of the families Limacidae and Milacidae in Australia, with two new records. *Journal of the Malacological Society of Australia* 3: 63-80.

PITFALL TRAPPING FOR SURVEYING ANT ASSEMBLAGES: LESSONS FROM A STUDY AT MOUNT PIPER, VICTORIA

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Abstract

Hinkley, S. And New, T.R., 1997. Pitfall trapping for surveying ant assemblages: lessons from a study at Mount Piper, Victoria. *Memoirs of the Museum of Victoria* 56: 369–376.

Ants were sampled by grids of pitfall traps from six main sites and four subsidiary sites at Mount Piper, Victoria, at intervals over a year. A total of 137 morphospecies, including representatives of 39 genera, were captured. Variations in catch between sites and seasons are discussed in relation to: completeness of sampling accomplished by pitfall traps; the amount of sampling effort needed to provide adequate inventory data; and possibilities of rapid sampling of ant assemblages. Short term sampling of ant assemblages may be inadequate for sound assessment of species diversity in assemblages.

Introduction

Surveys of ants of Mount Piper, Broadford, Victoria, (37°12'S, 145°00'E) have been an integral part of documenting the resource and critical habitat needs of rare Lycaenidae listed under Victoria's Flora and Fauna Guarantee Act 1988, and of defining the parameters of a 'Threatened Butterfly Community' (Jelinek et al., 1994; Britton et al., 1995, New et al., 1996). This isolated volcanic plug, reaching 456 m in altitude and being an enclave of natural woodland in a largely pastoral landscape, is now one of the most intensively surveyed areas for ants in Victoria. In this paper, we summarise results from a survey undertaken from March 1993–February 1994 and discuss their implications for survey design and interpretation. Aims of the survey, in addition to detecting ant hosts for *Acrodipsas* butterflies (Britton, 1997) were:

1. to determine the richness of the ant fauna of the Mount Piper educational reserve;
2. to assess distribution and diversity of ants at different sites in the reserve; and
3. to assess the amount of trapping needed to obtain reasonably accurate data on ant assemblages in the region.

Methods

Pitfall traps (plastic cups 7.4 cm diameter and 8.8 cm deep) were used in grids of 20 (5 × 4, 5 m spacing between traps — see Andersen, 1990) at six main sites and four subsidiary sites (the latter not treated in detail here) in and near the reserve (Fig. 1). Traps contained 70% alcohol and

ethylene glycol and were emptied at approximately fortnightly intervals from March to September 1993 and again from November 1993 to February 1994 (Table 3). Each grid was treated as the sampling unit; ants were sorted and identified to genus and morphospecies using keys by Andersen (1991), Hölldobler and Wilson (1990), Shattuck (1992) and Bolton (1994). A voucher collection is held at La Trobe University. The sites were chosen as representative of the open woodland of the region (Table 2). Limited amounts of direct searching for ants were undertaken at all sites.

Results

Overview

The total ant fauna from the 10 sites comprised 137 morphospecies in 39 genera (Table 1), of which 127 morphospecies were captured in pitfall traps, and the other 10 found only by direct searching.

Each of sites 1–6 supported more than 50 morphospecies, and each site yielded taxa not captured at any other site. Over the 10 sites, 47 morphospecies were found only at single sites. By far the greatest number and richness of ants (71 morphospecies) occurred at site 1 (Table 3), but any trapping occasion yielded no more than half the species recorded overall from a site, sometimes considerably fewer. Numbers of species and individuals trapped declined considerably from June to September and samples over this period reflected lessened ant activity during winter: the seasonal extremes over the

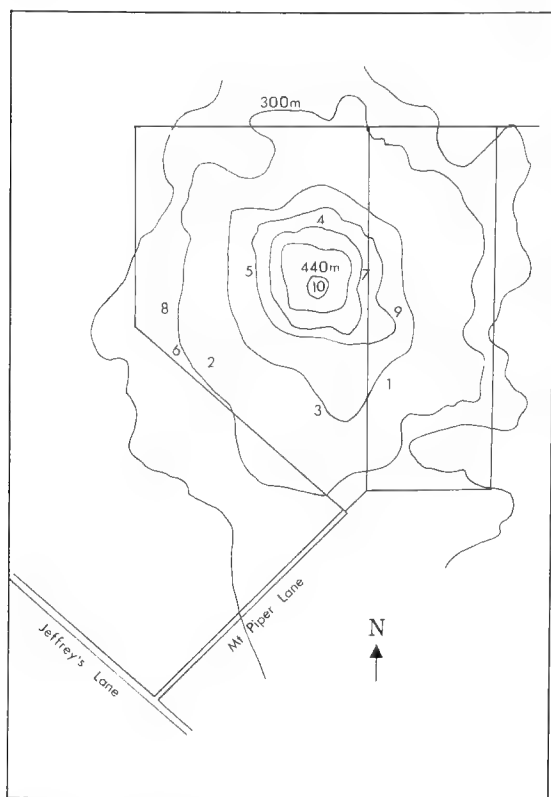


Figure 1. The Mount Piper reserve, showing sites 1-6, used for pitfall trapping grids in this survey, and sites 7-10, used for shorter-term augmentative survey.

survey were 3 morphospecies (site 3, September) and 32 morphospecies (site 1, December).

Species richness

Morphospecies accumulation curves for each site (Fig. 2) showed clear asymptotes by the end of the initial sampling period, implying (by current standards) that sampling had been effective. However, resumption of sampling led to capture of further species at all sites and 'new' ants were accumulated progressively through the second trapping period. The last samples taken at four of the six sites provided morphospecies new to those sites and, at two, to the entire survey.

Site complexity

Number of morphospecies plotted against the 'habitat complexity score' (Fig. 3) gave no clear relationship between these parameters. Nevertheless, the pattern of the sites was changed somewhat by comparing the total sample with the first sampling period. Site 1 became relatively richer, and site 3, not as disparate.

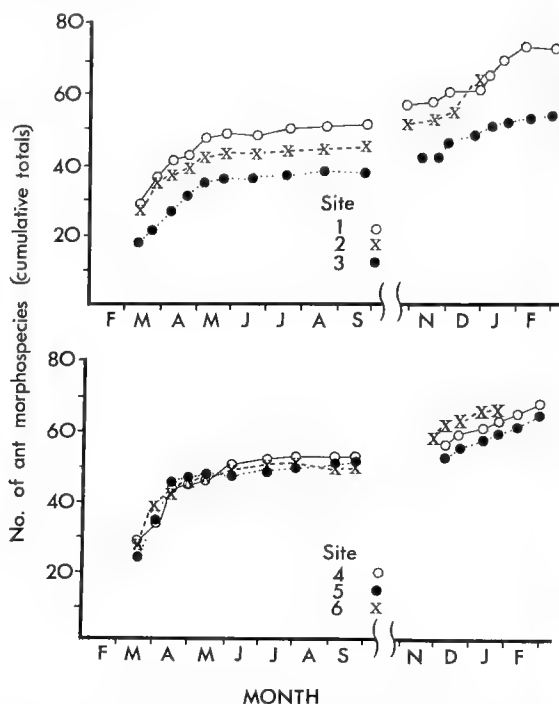


Figure 2. Accumulation curves for ant morphospecies from pitfall traps at sites 1-6 at Mount Piper, 1993-1994.

Site similarity

Jaccard's index of similarity ($[C_j = j/(a + b - j)]$, where j is the number of morphospecies common to sites A, B and a , b are the numbers of morphospecies in sites A, B, respectively; values range from 0 [no species in common] to 1 [all species shared]) was calculated for each pair of sites. The index (Table 4) confirmed that the spectrum of species at each site differed considerably, with only one site pair (2, 6) exceeding 0.5 over the whole sampling period. The mean Jaccard index value for each site against all others was not clearly related to species richness, but these values declined as sampling proceeded (Fig. 4), suggesting that increased sampling effort revealed greater relative distinctiveness of the ant fauna at each site as decreased similarity with any other site.

'Dominant' species

The most abundant morphospecies at each site (Table 5) and the number of traps in which a species was captured on each occasion (a measure of dominance which, in part, overcomes the bias due to numbers alone), differed considerably at different sites, both in the species involved and the duration/extent of

Table 1. Number of ant morphospecies from each genus, and the number of morphospecies from each genus found only at one site, collected by pitfall trapping and direct sampling at Mt Piper (* denotes 1, or if number in parentheses, more, morphospecies found only by direct sampling).

Subfamily	Genus	Total	No. found at 1 site
Myrmeciinae	<i>Myrmecia</i> *	15	7
Myrmicinae	<i>Aphaenogaster</i>	1	—
	<i>Colobostruma</i>	1	—
	<i>Crematogaster</i> *	2	1
	<i>Epopostruma</i>	3	3
	<i>Mayriella</i>	1	1
	<i>Meranoplus</i>	1	—
	<i>Monomorium</i>	4	—
	<i>Orectognathus</i>	1	—
	<i>Pheidole</i>	2	—
	<i>Podomyrma</i> *	6	4
	<i>Strumigenys</i>	1	—
	<i>Tetramorium</i>	3	2
Ponerinae	<i>Amblyopone</i>	5	1
	<i>Discothyrea</i>	1	1
	<i>Heteroponera</i>	1	—
	<i>Hypoponera</i>	3	2
	<i>Cerapachys</i>	1	—
	<i>Ponera</i> *	2	1
	<i>Rhytidoponera</i>	4	—
Formicinae	<i>Camponotus</i> *(3)	20	9
	<i>Melophorus</i>	11	5
	<i>Myrmecorhynchus</i>	1	—
	<i>Notoncus</i>	4	—
	<i>Paratrechina</i>	3	1
	<i>Plagiolepis</i>	1	—
	<i>Polyrachis</i>	5	2
	<i>Prolasius</i>	5	1
	<i>Pseudonotoncus</i>	1	—
	<i>Stigmatoceros</i>	10	3
Dolichoderinae	<i>Dolichoderus</i> *	3	1
	<i>Iridomyrmex</i> *	8	4
	<i>Doleromyrma</i>	1	—
	<i>Anonychomyrma</i>	1	—
	<i>Ochetellus</i>	1	—
	<i>Papyrius</i>	1	1
	<i>Leptomyrmex</i>	1	—
	<i>Tapinoma</i>	1	—
	<i>Technomyrmex</i>	1	—

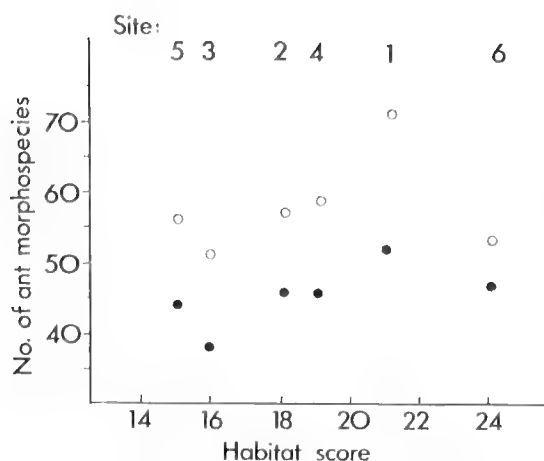


Figure 3. Number of ant morphospecies in pitfall traps plotted against habitat complexity score for initial (solid spots) and total (open circles) trapping periods. (Habitat complexity assessed from: canopy cover [1–5, increasing 20 % intervals from 0–100]; structural diversity of vegetation [1–5: 1 (grass only), 2 (grass and trees), 3 (grass, trees, shrubs), 4 (grass, trees, shrubs, ground covers), 5 (grasses, trees, small trees, shrubs, ground covers)]; litter, dry weight (1–5: successive 50 g counts on 30 cm squares); rocks (1–5: 1 (none), 2 (few), 3 (numerous, even-sized), 4 (numerous, two or more sizes), 5 (very numerous)], vascular plant richness (1–5: successive accumulations of 6 spp.); bare ground [1–5, increasing 20% intervals from 0–100]; in sequence for each site scores are (1) 4, 5, 2, 2, 5, 2, (2) 2, 4, 2, 3, 5, 2, (3) 3, 4, 1, 3, 4, 1, (4) 2, 2, 2, 5, 4, 3, (5) 2, 3, 1, 4, 5, 1, (6) 3, 5, 3, 3, 4, 4].

dominance, reflecting seasonal patterns of activity. Thus, although *Aphaenogaster longipes* was the most abundant species at site 2 for the first 10 sampling occasions, it was then supplanted by other taxa. Collectively, 13 morphospecies are included as 'most abundant ants', and 12 as 'most frequently trapped' in these rankings.

Discussion

Andersen's (1993) designation of ants as 'arguably the most important faunal group in the Australian environment' was prompted by series of studies on ant assemblage in many parts of the country, and the realisation that functional group analysis (included for this survey in New et al. 1996) can provide considerable ecological information of great value in conservation assessment. Increased emphasis and interest in rapid measurement of diversity has recently prompted investigation of use for short-

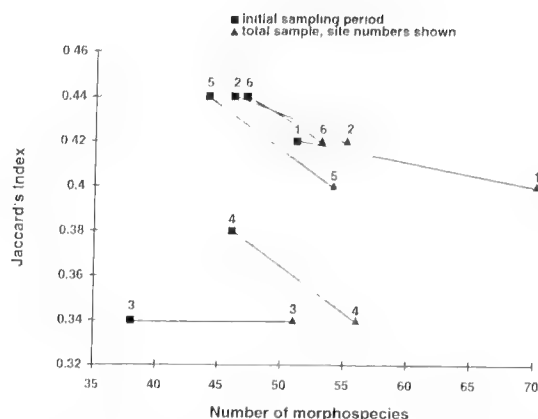


Figure 4. Jaccard's index of similarity against number of ant morphospecies at each site for initial and total trapping periods.

term surveys of ants, mainly using pitfall traps as the prime sampling method — in itself open to severe reservation and difficulty of standardisation (Andersen 1990, Majer, 1997).

The survey reported here has led to Mount Piper having one of the best-documented ant assemblages in Victoria, and a morphospecies diversity which is apparently unusually high for the region. The high richness is much more representative of arid areas than of mesic Victoria, and may reflect the meeting of the ant faunal sets, as Mount Piper is near the boundary of these regions. More than 150 species of ants can occur on small areas in the northwest mallee region (Andersen, 1984), and the outlying Long Forest mallee near Melton supports 77 species in 21 genera (Andersen et al., 1991) and, like Mount Piper, shows aspects of the interaction of Bassian and Eyrean ant faunas. Including surveys by Miller and New (1997) and related collections (New et al. 1996), Mount Piper and its immediate environs are known to harbour at least 145 ant morphospecies including a very high proportion of the genera recorded from southeast Australia; and it is likely that further taxa (such as cryptic taxa not amenable to pitfall trapping) also occur.

However, the intensity of sampling for this survey has been considerably higher than that in many related assessments of ants (summarised by Andersen, 1995), and some important points emerge in relation to site evaluation and sampling adequacy.

In particular, the question of 'how much sampling is enough?' is becoming critical in

Table 2. Measurements for a number of environmental parameters at ant trapping sites 1–6 on Mount Piper.

Aspect	SITE					
	1	2	3	4	5	6
	SE	SSW	SSE	N	WSW	SW
Altitude (approx. m)	270	270	360	360	360	270
Canopy cover (%)	70	40	60	40	25	50
Area of bare ground (%)	25	40	5	55	10	65
Ground covers (%)	2	3	5	0	6	2
Grasses/herbs (%)	61	35	82	40	77	2
Shrubs (%)	5	15	3	0	0	25
Trees (%)	7	7	5	5	7	6
No. of plant species	25	28	21	21	26	23
Rocks	scarce	very few large, many small	many hand sized	all sizes and numerous	common, but < site 4	numerous hand sized
Leaf litter (g/30 cm ² , dry weight)	83.9	61.9	47.1	76.8	40.2	130.3

invertebrate conservation assessment, be it for inventory (i.e. seeking to capture as many species as possible, including rare taxa) or to assess representativeness or 'typicalness' (i.e. seeking to define the 'most usual' taxa living in an area and which may be used to define the condition of a habitat or site). At present, Mount Piper, appears to have many highly localised and rare species. The key points include:

1. that any single sample retrieved only a small proportion of the taxa associated with a site;
2. that each of the six sites had a distinctive ant complement, so that a single plot could not represent the greater area adequately;
3. that increased sampling effort changed perception of the ant assemblage of each site and the extent of similarity of different sites;
4. rendered each site more distinctive; and
5. that seasonal variability in catches may influence accumulation curves used to interpret sampling adequacy.

These points counsel against uncritical adoption of rapid pitfall surveys for ants and suggest the need for appraisal of these in relation to long

term trapping surveys. Olsen (1991) suggested that obtaining 75 % of the species present constitutes a 'reasonable sample success', but this (or any similar proportional figure) can be defined only with hindsight. For most of the sites investigated here, this level was reached after 3–5 sampling occasions in summer, but at site 3 was not achieved during the whole of the first sampling period. The heterogeneity between assemblages at the different sites implies a mosaic pattern of ant taxa in the region, leading us to echo Samways' (1990) plea for longterm studies of ant assemblages, even to define the relativity between apparently similar sites for ranking purposes or for faunal documentation. Cross-season sampling and extensive sampling over warmer parts of the year are needed to accumulate even reasonably complete species listings.

Despite widespread (and, sometimes, wishful) advocacy, in the interests of promoting rapid biodiversity assessment, that ant assemblages can be defined adequately over short term surveys, there is clear implication that this may not always be so.

Table 3. Numbers of ant morphospecies and individuals (given as 'species/individuals' captured in pitfall traps at Mount Piper at sites 1–6, 1993–1994.

Sampling date		Site					
sites 1–3	sites 4–6	1	2	3	4	5	6
10.iii	14.iii	27/1059	28/733	17/821	25/460	21/855	25/1049
21.iii	28.iii	29/675	27/314	13/194	28/555	26/531	25/789
5.iv	12.iv	29/448	22/354	16/259	26/405	24/384	25/418
19.iv	26.iv	25/378	24/274	17/207	29/568	22/318	26/395
3.v	9.v	26/316	25/280	17/156	21/389	16/181	21/270
19.v	31.v	16/88	16/175	12/71	18/137	13/45	18/98
13.vi	1.vii	6/18	7/44	5/12	12/74	9/23	13/69
12.vii	27.vii	7/15	9/46	5/23	15/34	5/14	10/75
12.viii	25.viii	5/12	9/41	7/23	9/37	9/27	12/51
10.ix	10.ix	12/27	15/45	3/19	12/75	8/33	16/50
(all) 26.xi		25/661	21/411	—	—	—	23/282
7.xii		19/717	23/194	17/362	27/666	12/70	26/455
17.xii		32/1239	24/377	18/325	29/489	28/338	22/542
3.i		23/1933	25/394	21/311	24/305	—	24/491
16.i		29/1655	—	18/283	—	26/586	15/151
30.i		31/1549	—	16/435	21/463	26/502	—
14.ii		28/1021	—	15/218	25/552	23/405	—
28.ii		23/557	—	8/99	22/405	19/439	—
Total no.		71	57	51	59	56	53
No. only at site		6	4	8	7	6	4

Table 4. Jaccard's index (C_j), calculated using the total results of the total sampling period, for ant morphospecies collected from sites 1–6 at Mt Piper.

Site	1	2	3	4	5	6
1	—					
2	0.47	—				
3	0.34	0.29	—			
4	0.30	0.36	0.31	—		
5	0.41	0.38	0.41	0.39	—	
6	0.48	0.55	0.34	0.35	0.40	—
Mean	0.40	0.42	0.34	0.34	0.40	0.42

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Table 5. Most common ant morphospecies collected from sites 1–6 on Mt. Piper over first 10 sampling periods (Feb.–Sept. 1993) and in later sampling.

Site	Most common morphospecies	Sampling period									
		1	2	3	4	5	6	7	8	9	10
1	<i>Rhytidoponera victoriae</i>	✓	✓	✓	✓	✓	✓	✓			✓
	<i>Pheidole</i> sp. 1								✓	✓	
2	<i>Aphaenogaster longiceps</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
3	<i>Rhytidoponera victoriae</i>	✓	✓	✓	✓	✓	✓				✓
	<i>Prolasius pallidus</i> sp. 1							✓			
	<i>Monomorium leae</i>								✓	✓	
4	<i>Pheidole</i> sp. 1	✓	✓		✓	✓	✓	✓		✓	
	<i>Rhytidoponera tasmaniensis</i>			✓							
	<i>Tapinoma minutum</i>								✓		✓
5	<i>Rhytidoponera victoriae</i>	✓	✓	✓	✓						
	<i>Aphaenogaster longiceps</i>					✓	✓	✓	✓	✓	
	<i>Notoncus hickmani</i>								✓		
	<i>Pheidole</i> sp. 2										✓
6	<i>Rhytidoponera victoriae</i>	✓									
	<i>Aphaenogaster longiceps</i>		✓	✓	✓	✓	✓	✓	✓	✓	✓
		11	12	13	14	15	16	17	18		
1	<i>Plagiolepis</i> sp.	✓									
	<i>Anonychomyrma itinerans</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	
2	<i>Plagiolepis</i> sp.	✓				✓					
	<i>Crematogaster</i> sp.		✓	✓							
3	<i>Crematogaster</i> sp.	✓									
	<i>Plagiolepis</i> sp.		✓								
	<i>Rhytidoponera victoriae</i>			✓	✓	✓	✓	✓	✓	✓	
4	<i>Crematogaster</i> sp.	✓									
	<i>Monomorium</i> sp. 1		✓	✓							
	<i>Pheidole</i> sp. 1				✓	✓	✓				
5	<i>Plagiolepis</i> sp.	✓									
	<i>Rhytidoponera victoriae</i>		✓	✓	✓	✓	✓				
6	<i>Plagiolepis</i> sp.	✓	✓	✓							
	<i>Rhytidoponera victoriae</i>				✓	✓					

References

- Andersen, A.N., 1984. Community organisation of ants in the Victorian mallee. *Victorian Naturalist* 101: 248–51.
- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–57.
- Andersen, A.N., 1991. *The ants of southern Australia*. CSIRO, Melbourne.
- Andersen, A.N., 1993. Ant communities in the Gulf region of Australia's semi-arid tropics: species composition, patterns of organisation, and biogeography. *Australian Journal of Zoology* 41: 399–414.
- Andersen, A.N., 1995. Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biological Conservation* 73: 39–43.
- Andersen, A.N., Myers, B.A. and Buckingham, K.M., 1991. The ant fauna of a mallee outlier near Melton, Victoria. *Proceedings of the Royal Society of Victoria* 103: 1–6.
- Bolton, B., 1994. *Identification guide to the ant genera of the world*. Harvard University Press: Cambridge, Mass.
- Britton, D.R., 1996. Ant trap nests enable detection of a rare localised butterfly, *Acrodipsas myrmecophila* (Waterhouse and Lyell) (Lycanidae) in the field. *Memoirs of the Museum of Victoria* 56: 383–387.

- Britton, D.R., New, T.R. and Jelinek, A., 1995. Rare Lepidoptera at Mount Piper, Victoria — the role of a threatened butterfly community in advancing understanding of insect conservation. *Journal of the Lepidopterists' Society* 49: 97–113.
- Hölldobler, B. and Wilson, E.O., 1990. *The ants*. Belknap Press: Cambridge, Mass.
- Jelinek, A., Britton, D.R. and New, T.R., 1994. Conservation of a 'threatened butterfly community' at Mount Piper, Victoria. *Memoirs of the Queensland Museum* 36: 115–20.
- Majer, J.D., 1997. The use of pitfall traps for sampling ants — a critique. *Memoirs of the Museum of Victoria* 56: 323–329.
- Miller, L.J. and New, T.R., 1997. Mount Piper grasslands: pitfall trapping of ants and interpretation of habitat variability. *Memoirs of the Museum of Victoria* 56: 377–381.
- New, T.R., Britton, D.R., Hinkley, S. and Miller, L.J., 1996. The ant fauna of Mount Piper, and its relevance to environmental assessment and the conservation of a threatened invertebrate community. *Flora and Fauna, Technical Report No. 143*.
- Olsen, D.M., 1991. A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a tropical wet forest, Costa Rica. *Biotropica* 23: 166–72.
- Samways, M.J., 1990. Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. *Oecologia* 84: 482–90.
- Shattuck, S.O., 1992. Generic revision of the ant subfamily Dolichoderinae (Hymenoptera: Formicidae). *Sociobiology* 21: 1–181.

MOUNT PIPER GRASSLANDS: PITFALL TRAPPING OF ANTS AND INTERPRETATION OF HABITAT VARIABILITY

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Abstract

L.J. Miller and New, T.R., 1997. Mount Piper grasslands: pitfall trapping of ants and interpretation of habitat variability. *Memoirs of the Museum of Victoria* 56: 377-381.

Ants were sampled by pitfall trapping in grassland patches near Mount Piper education reserve, Victoria. Ten surveys, from February to July 1994, yielded 18 genera and 36 morphospecies, with considerable differences between the seven sites. The results suggested highly localised mosaic variation with respect to different functional groups. Ranking of sites on generic diversity usually coincided with morphospecies on most of the sites, from the 'most natural' to the 'most degraded' and the more abundant and widespread ants constitute a core taxon suite which can grossly characterise the ant assemblage of the grasslands.

Introduction

The rationale of ant surveys at Mount Piper, Broadford, Victoria, was outlined by Hinkley and New (1997) as a component of defining the conservation needs of rare lycaenid butterflies whose caterpillars are myrmecophilous (see also Britton et al., 1995). Searches for particular ant species have been extended beyond the central reserve area into adjacent properties, and this paper focuses on one of these, the 100 ha block 71C along the eastern border of Mount Piper (Fig. 1). The block contains substantial areas of grassland, and has been grazed heavily by domestic stock (predominantly sheep) and kangaroos. Many of the grassland patches are separated by eucalypt-wooded ridges, and some have been invaded by exotic plants, predominantly the grass *Holcus lanatus*. This paper reports an attempt to define the ant fauna of these grasslands, as an adjunct to the survey of the Mount Piper reserve by Hinkley and New, and to assess and compare the ant assemblages of 'more natural' and 'more disturbed' grassland patches to determine the extent of heterogeneity over the area and evaluate the worth of ants as indicators of grassland disturbance, manifest by invasion by exotic grass species.

Methods

Five sites, two subdivided to provide a total of seven trapping areas, were used for placement of pitfall traps (plastic cups 7.4 cm diameter, 8.8 cm deep) in grids of 20 (5 × 4, 5 m spacing

between traps) over the period February-July 1994. Traps contained 70% alcohol and ethylene glycol, and were emptied at approximately fortnightly intervals so that trapping was continuous over the survey period. Ants were separated and identified to genus and morphospecies using

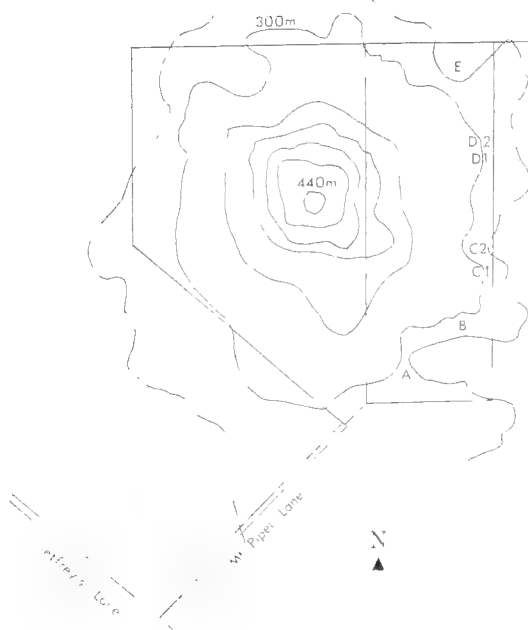


Figure 1. Mount Piper and Block 71C (the rectangular area to the right (east) of the mountain), showing sites A-E, used for pitfall trapping grids in this survey.

keys by Andersen (1991), Hölldobler and Wilson (1990), Shattuck (1992), Bolton (1994) and several revisionary studies. The five sites (A–E in Fig. 1, with C₁, C₂ and D₁, D₂ representing separate grids within the topographically complex sites C and D) had all been grazed heavily by sheep in the year preceding the survey. Direct searches for ants were also made on each site.

Sites were ranked on 'degree of disturbance', representing separate vegetation cover and predominance of native grasses (*Danthonia*) or exotic *Holcus* (equated to higher disturbance). In sequence from 'most natural' to 'most disturbed', the sequence is D₂, C₁, A (native grasses), D₁/E, C₂, B (*Holcus*) so that two contrasting series are included.

Analysis is noted in context. Allocation to functional groups (at generic level) follows Andersen (1990).

Results

Overview

The 12161 ants captured (Table 1) included 36 morphospecies and representatives of 20 genera. Considerable variation occurred on all seven trapping grids, and 11 morphospecies were recorded only at single sites.

Iridomyrmex vicina comprised more than 60% of all ants captured and, at the other extreme, eight morphospecies were represented by individuals. Direct searching did not yield any species not captured by the traps. Analysis by frequency of capture, rather than simple abundance, implied less domination by *I. vicina*. Ranking species by 'trapping events' (7 sites × 10 occasions = 70 trapping events, treating a grid as a sampling unit) gave the sequence of *Pheidole* sp. (59 events), *Rhytidoponera tasmaniensis* (53), *Camponotus consobrinus* (41), *I. vicina* (37). *R. tasmaniensis* comprised only 5.7% of total ants and *Pheidole*, nearly 16%.

Diversity differed between sites. At the extremes, site A yielded 30 morphospecies in 16 genera and site E, 11 morphospecies in 7 genera. Ranking of sites by generic diversity (high-low: A, C₂, C₁, D₁/D₂, B/E) partially coincided with ranking by species diversity (A, C₂, C₁, B, D₂, D₁, E), especially for the richer sites.

New species and site records accumulated throughout the survey, but a high proportion of taxa (26/36 morphospecies) occurred in the first two-week period, with the highest augmentation (four morphospecies) in the next fortnight. Two morphospecies were detected for the first time in the last trapping period. In general, and reflect-

ing seasonal activity, ant diversity was greatest early in the trapping sequence and genus and species richness declined to about half the peak levels over intervals 8 and 9 (Table 2). Extremes over the survey were 13 genera/27 morphospecies (interval 2) and five genera/10 morphospecies (interval 8). Incidence of particular taxa also varied over the course of the survey. As examples, *Stigmacros* occurred only in the first five trap sets, and *Melophorus* and *Meranoplus* were absent in sets 8–10. *Stigmacros* occurred only at site A, and in small numbers, whereas *Melophorus* showed a clear pattern of declining activity manifest in the number of sites (a) and the number of individuals captured (b), so that a/b for successive intervals from 1 was 5/96, 4/35, 3/27, 1/1, 3/6, 0/0, 1/1.

Site condition

The three native sites supported 30 (A), 20 (C₁) and 14 (D₂) ant morphospecies, and the four *Holcus* sites had 17 (B), 22 (C₂), 13 (D₁) and 11 (E), so that the range of values in each series is high, and the series overlap. The paired and contrasting C and D subsites, only a few tens of metres apart, did not differ significantly from each other in diversity: C₁ and C₂ shared 14 (of 26) morphospecies, and D₁ and D₂ 10 (of 18). Ten species occurred on all three native sites, and a further 10 were found on two of them. Six of the former group were trapped also on all four *Holcus* sites, these species being *I. vicina*, *C. consobrinus*, *C. myoporinus*, *Melophorus*, *R. tasmaniensis* and *Pheidole*. Three (*I. gracilis*, *Notoncus enormis*, *Monomorium*) were found on two of them. The tenth (*Meranoplus*) was found on only one *Holcus* site, but was also uncommon on the *Danthonia* sites.

N. ectatommoides occurred on all four *Holcus* sites and two native sites, and *R. victoriae* on two sites in each category. Fifteen of 16 taxa (the sole exception being *Polyrhachis*) on two, three or four *Holcus* sites were found also on two or three native sites. Total representation was 33 morphospecies (native sites) and 28 morphospecies (*Holcus* sites).

Species shared between each pair of sites (Table 3) were usually a high proportion of the total for the sites and values for a simple Sorenson index of similarity are correspondingly high (Table 3). The ants of site E are fully a subset of those at A and C₂; the highest similarity is between sites E/D₁ and the lowest between C₁/E. Ranking of sites by diversity differed between sampling occasions (Table 2).

Table 1. Grassland ants at Mount Piper, 1994: species list and incidence (✓) at each trap site (A-E). Taxa represented by single individuals are underlined.

	A	B	C ₁	C ₂	D ₁	D ₂	E	No. sites
<i>Myrmecia</i> 'picta'	✓		✓	✓				3
<i>M.</i> 'pilosula'	✓		<u>✓</u>		<u>✓</u>			3
<i>Meranoplus</i>	✓		<u>✓</u>	✓		<u>✓</u>		4
<i>Mayriella</i>	✓							1
<i>Podomyrma</i>					<u>✓</u>			1
<i>Pheidole</i>	✓	✓	✓	✓	<u>✓</u>	✓	✓	7
<i>Monomorium</i>	✓		✓	✓		✓	✓	5
<i>Polyrhachis</i>	✓	<u>✓</u>		✓				3
<i>Camponotus</i> 'claripes'	✓	<u>✓</u>	✓	✓	✓		<u>✓</u>	6
<i>C.</i> 'consobrinus'	✓	✓	✓	✓	✓	✓	<u>✓</u>	7
<i>C.</i> 'innexus'	✓		<u>✓</u>	✓				3
<i>C.</i> 'intrepidus'		<u>✓</u>						1
<i>C.</i> 'myoporus'	✓	<u>✓</u>	✓	✓	✓	✓	<u>✓</u>	7
<i>C.</i> 'nigroaeneus'	✓	✓	✓	<u>✓</u>				3
<i>C.</i> 'suffusus'	<u>✓</u>							1
<i>C.</i> 'rubiginosus'	<u>✓</u>	✓						2
<i>C.</i> sp.	✓	✓	✓	✓				4
<i>Stigmacros</i>	✓							1
<i>Myrmecorhynchus emeryi</i>	<u>✓</u>							1
<i>Notonocus</i> 'enormis'	✓	✓	✓		<u>✓</u>	✓		5
<i>N.</i> 'ectatommoides'	✓	<u>✓</u>		✓	<u>✓</u>	<u>✓</u>	✓	6
<i>Melophorus</i>	✓	✓	✓	✓	✓	✓	✓	7
<i>Amblyopone</i>	<u>✓</u>							1
<i>Rhytidoponera</i> 'aspera'				✓		✓		2
<i>R.</i> 'tasmaniensis'	✓	✓	✓	✓	✓	✓	✓	7
<i>R.</i> 'metallica'	<u>✓</u>			✓	✓	✓	<u>✓</u>	5
<i>R.</i> 'victoriae'	<u>✓</u>	✓	✓	✓				4
<i>Platythyrea</i>			<u>✓</u>					1
<i>Heteroponera</i>	<u>✓</u>							1
<i>Dolichoderus</i> 'doriae'				<u>✓</u>				1
<i>Leptomyrme</i> 'erythrocephalus'	<u>✓</u>							1
<i>Iridomyrmex</i> 'bicknelli'	✓	✓	<u>✓</u>					3
<i>I.</i> 'gracilis'	✓	✓	<u>✓</u>	✓		✓		5
<i>I.</i> 'purpureus'	<u>✓</u>			✓	✓	✓	✓	5
<i>I.</i> 'vicina'	<u>✓</u>	✓	✓	✓	✓	✓	✓	7
<i>Doleromyrma darwinianus</i>				<u>✓</u>	✓			2

Table 2. Ant richness (no. of genera/no. of species) at each grassland site (A–E) and sampling occasion (1–10, as fortnightly intervals from February–July) near Mount Piper, 1994.

Site	Sampling occasion (genera/species)									
	1	2	3	4	5	6	7	8	9	10
A	12/20	11/21	11/17	8/15	9/15	5/8	6/10	3/3	3/3	6/9
B	6/12	6/11	6/11	5/10	6/8	6/10	5/10	4/6	4/5	4/6
C ₁	7/11	8/14	9/15	5/6	4/5	3/5	8/12	4/6	2/2	6/10
C ₂	8/14	7/15	5/9	6/9	5/6	6/7	5/8	5/6	3/4	4/4
D ₁	6/9	5/8	5/6	0/0	3/3	6/7	5/8	3/3	4/5	5/7
D ₂	6/10	7/12	4/4	5/5	5/7	3/3	4/6	2/2	0/0	2/3
E	4/4	7/7	1/1	1/1	5/6	2/2	2/2	3/3	2/2	5/5
All	12/26	13/27	11/22	10/20	10/20	8/18	9/21	5/10	6/10	9/16

Table 3. Number of species of ant (top) and Sorenson index of similarity ($S = 2j/a+b$, where j is number of shared species and a, b , are number of species in A, B, bottom) shared between grassland sites (A–E), Mount Piper 1994.

	No. shared species						
	A	B	C ₁	C ₂	D ₁	D ₂	E
A		16	17	19	12	13	11
B	0.68		13	13	9	9	8
C ₁	0.68	0.70		16	10	10	8
C ₂	0.73	0.67	0.76		10	13	11
D ₁	0.56	0.60	0.61	0.57		10	10
D ₂	0.59	0.58	0.59	0.72	0.74		10
E	0.54	0.57	0.52	0.67	0.83	0.80	

Table 4. Functional grouping of ant species from grassland sites A–E, given as number (%) of total species.

Functional Group	Site							
	A	B	C ₁	C ₂	D ₁	D ₂	E	Total
Dominant <i>Iridomyrmex</i>	5(18)	4(22)	4(20)	3(14)	1(8)	4(26)	2(20)	6(17)
Subordinate 'Camponotinae'	9(32)	8(44)	6(39)	7(33)	3(23)	2(13)	3(30)	10(28)
Hot climate specialists	2(7)	1(5.5)	2(10)	2(10)	1(8)	2(13)	1(10)	2(5.5)
Cold climate specialists	3(11)	2(11)	1(5)	1(5)	3(23)	2(13)	1(10)	4(11)
Cryptic	1(3.5)	—	—	1(5)	—	—	—	2(5.5)
Subcryptic	2(7)	—	—	—	—	—	—	2(5.5)
Opportunists	4(14)	2(11)	2(10)	4(20)	3(23)	3(20)	2(20)	5(14)
Generalised Myrmicinae	2(7)	1(5.5)	2(10)	2(10)	1(8)	2(13)	2(20)	2(5.5)
Large solitary foragers	1(3.5)	—	3(15)	1(5)	1(8)	—	—	3(8)

Functional groups

Analysis of functional groups (Table 4) revealed few major differences between the most natural and most disturbed sites by the most abundant groups. 'Subordinate Camponotinae' were the predominant group at five sites, co-predominant at one (with 'opportunists' at D) and was minor only at D₂. Cryptic and subcryptic taxa were scarce or absent, perhaps in part because they are not amenable to pitfall trapping. 'Large solitary foragers' (*Myrmecia*) were poorly represented throughout the series.

Discussion

The ant morphospecies found are a subset of the ants trapped in nearby wooded areas (Hinkley and New, this volume) and only one additional species (*Rhytidoponera* 'metallica') was found on the grasslands. The assemblages are far less diverse than those on woodland sites, and most grassland sites supported fewer than 20 species (maximum of 30 at A). Unlike the woodland survey a high proportion of taxa was captured very early in the trapping sequence and (neglecting singleton incidences — Table 1), many species occurred on several sites with little apparent discrimination in relation to dominant grass species. However, because of the previous grazing history, it is likely that all sites are 'disturbed' and the broad range of such species may simply reflect that they are not specialised ecologically and that the assemblages may formerly have been more diverse. *Rhytidoponera*, for example, are 'opportunistic' taxa, and *R. tasmaniensis* was widespread. Overall disturbance may be more significant to ants than simple replacement of native by exotic grass species. However, these assemblages appear to be easier to sample and define than are the more diverse woodland faunas — but no second sampling sequence equivalent to that taken by Hinkley and New was undertaken, and such inferences must remain tentative. Indeed, *Rhytidoponera* are often dominant as broadly adapted species in mesic ant assemblages (such as at Wilsons Promontory; Andersen 1986a, b).

Nevertheless, it is clear that the same ant species occurred in grossly similar ecological balance (as indicated by functional groups) on the seven sites. It is possible to define a 'core taxon suite' which can be used to define the ant

assemblages of grasslands in this region and constitute a basis for comparison with other grassland sites, but also to recognise that the mosaic nature of such assemblages will assure that many highly localised morphospecies will be present and render each site distinct from others. Because such variation is hard to quantify without extensive sampling, surveys of grassland ants should include trapping at several sites even if the vegetation appears to be homogeneous throughout the area.

Acknowledgments

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References

- Andersen, A.N., 1986a. Patterns of ant community organization in mesic southeastern Australia. *Australian Journal of Ecology* 11: 87–97.
- Andersen, A.N., 1986b. Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in southeastern Australia. *Australian Journal of Zoology* 34: 53–64.
- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–57.
- Andersen, A.N., 1991. *The ants of southern Australia*. CSIRO: Melbourne.
- Bolton, B., 1994. *Identification guide to the ant genera of the world*. Harvard University Press: Cambridge, Mass.
- Britton, D.R., New, T.R. and Jelinek, A., 1995. Rare Lepidoptera at Mount Piper, Victoria — the role of a threatened butterfly community in advancing understanding of insect conservation. *Journal of the Lepidopterists' Society* 49: 97–113.
- Hinkley, S. and New, T.R., 1997. Pitfall trapping for surveying ant assemblages: lessons from a study at Mount Piper, Victoria. *Memoirs of the Museum of Victoria* 56: 369–376.
- Hölldobler, B. and Wilson, E.O., 1990. *The ants*. Belknap Press: Cambridge, Mass.
- Shattuck, S.O., 1992b. Generic revision of the ant subfamily Dolichoderinae (Hymenoptera: Formicidae). *Sociobiology* 21: 1–181.

ANT TRAP NESTS ENABLE DETECTION OF A RARE AND LOCALISED BUTTERFLY,
ACRODIPSAS MYRMECOPHILA (WATERHOUSE AND LYEELL)
(LEPIDOPTERA: LYCAENIDAE) IN THE FIELD

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Abstract

Britton, D.R., 1997. Ant trap nests enable detection of a rare and localised butterfly, *Acrodipsas myrmecophila* (Waterhouse and Lyell) (Lepidoptera: Lycaenidae) in the field. *Memoirs of the Museum of Victoria* 56(2): 383-387.

Location of the ant *Papyrius nitidus* is essential in order to determine critical habitat for the rare butterfly *Acrodipsas myrmecophila*, which is known in Victoria from a single locality (Mount Piper). This paper describes the location of *P. nitidus* colonies at Mount Piper and the subsequent detection of immature stages of *A. myrmecophila* in a *P. nitidus* colony. The benefits of trap nests for detection, observation and conservation of the ant/butterfly association are outlined and discussed.

Introduction

The Small Ant-blue, *Acrodipsas myrmecophila* (Waterhouse and Lyell), is a rare butterfly in Victoria, and is scarce and localised throughout the rest of Australia. It has a single current Victorian locality at Mount Piper (32°12'S, 145°0'E), where occasional adult individuals have been taken from the summit of the mount since 1978 (D. F. Crosby, pers. comm.). This butterfly species and the related species, *A. brisbanensis* (Miskin) are listed as threatened on Schedule 2 of Victoria's Flora and Fauna Guarantee Act, 1988. These two species, and associated biota, form the basis of Butterfly Community No.1, a butterfly community listed as threatened on Schedule 2 of the same Act (Jelinek, 1991; Britton et al., 1995).

A. myrmecophila has a symbiotic relationship with an ant species *Papyrius nitidus* (Mayr). The larvae and pupae of the butterfly occur in nests of this ant, and the larvae are thought to be myrmecophagous (Common and Waterhouse, 1981) as is the closely related *A. illidgei* (Waterhouse and Lyell) (Sampson, 1989). The adults of most *Acrodipsas* spp., particularly males, congregate on hill-tops; several species are known only from adults collected from hill-tops (Common and Waterhouse, 1981).

A. myrmecophila has been recorded from only a few Victorian localities, all of which have suffered from changes in habitat. Colonies were known from Ocean Grove, Ringwood, Wandin, Heathmont and Broadford. The butterfly is almost certainly extinct at Ocean Grove,

Wandin, Heathmont and Ringwood, and the original colonies at Broadford have disappeared. It is also known from a few specimens taken at isolated localities (mostly hill-tops) in New South Wales, Queensland (including a single record from Cape York), and from a single record near Darwin, in the Northern Territory (Common and Waterhouse, 1981; Dunn and Dunn, 1991). A breeding colony has been recorded from Milmerran, Queensland (Common and Waterhouse, 1981), but the current status of this population is not known.

In order to prepare a sound management plan to conserve the population of *A. myrmecophila* at the Mount Piper locality it was necessary to determine the critical habitat for this species; this formed part of the recovery plan (research phase) for Butterfly Community No. 1 (Jelinek, 1992). Presence of the host ant, *Papyrius nitidus*, is an essential requirement for the butterfly. *P. nitidus* has been the target of concerted search efforts by researchers at Mount Piper for the past four years (Britton and New, 1992, 1993; Hinkley, 1993; New et al., 1994; Beardsell, 1994; Miller, 1994). Direct searches in farmland, roadside verges and bushland in and around the Mount Piper reserve have failed to locate ant colonies, as has pitfall trapping on the wooded slopes of the reserve and private land on the mountain (Britton and New, 1992; Hinkley, 1993), and in grasslands east of the reserve (Miller, 1994). These efforts have resulted in the collection of a large body of information about the ant communities present in the Mount Piper

region (New et al., in press) and butterfly communities (Britton et al., 1995).

This paper describes the successful location of *P. nitidus* and the subsequent discovery of immature stages of *A. myrmecophila* at Mount Piper, and describes some aspects of the distribution, biology and behaviour of *P. nitidus* and *A. myrmecophila*. The use of trap nests for survey and conservation research is described and discussed.

Methods

Surveys

Surveys in the 1994/95 season consisted of visually searching suitable areas as defined by Beardsell (1994). Previous work at Mount Piper included searches of the more heavily wooded slopes (Britton and New, 1992; 1993; New et al., 1994). Habitat requirements for *Papyrius nitidus* in other regions of Victoria are sunny and well-drained ridges and slopes under a tree stratum that does not exceed 25% projected foliage cover and on slopes that do not exceed 25% inclination (Beardsell, 1994). This excludes most of the Mount Piper Education Reserve, and some private land adjoining the reserve, hence most searches over the 1994–1995 season were in private land east, west and south-west of the mountain.

Design and construction of trap nests

The trap nests used in this study were based on a design by C. Beardsell. *Papyrius* spp. normally nest in dead wood, soil and at the base of living trees. The trap nests were designed to be attractive to the ants, and to provide a dry, safe space for the ants to nest in. The trap nests needed to be opened and inspected at regular intervals.

The nests were made from old hardwood. Care was taken to avoid wood that had been treated with any chemicals (e.g., creosote) that might deter or kill the ants. Old railway sleepers and fence strainers were used for the initial six trap nests, whose dimensions varied from 47 to 62 cm long, 11 to 32 cm wide, and 10 to 15 cm deep.

The trap nests were made by cutting the wood in half lengthwise. The bottom-half was then grooved to form nest cavities which were connected to the outside of the nest and each other by entrance tunnels (Figure 1). Trap nests were washed with a non-scented detergent (Truk-Wash) then left out in the sun for a week to bleach out traces of detergent which may be toxic to the ants. The two halves were held

together by metal straps and clamps (Emlocks, available from apiarists supplies).

Six trap nests were placed adjacent to saplings colonised by the ant in the eastern colony (4 Jan 1995) (Figure 2). The traps were inspected eight times between 6 Jan 1995 and 2 Mar 1995.

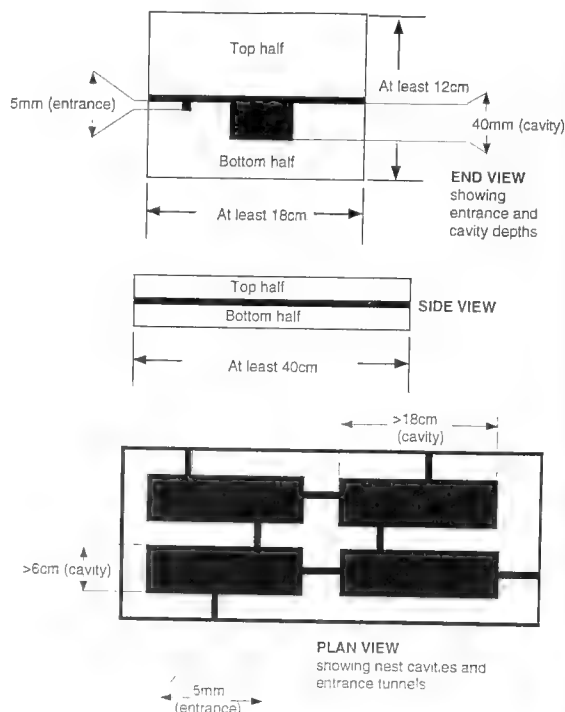


Figure 1. Schematic diagram of trap nests with approximate measurements. Diagram is not to scale.

Results

A *P. nitidus* colony, covering an area of about 25×15 m, was located in private land to the east of the reserve (23 Oct 1994), and was later found to harbour immature stages of the Small Ant Blue butterfly, *Acrodipsas myrmecophila*. The above ground portions of the colony consisted of a dead tree stump (39 cm wide, 38 cm high), some small flat pieces of wood adjacent to this stump and about six immature Red Box (*Eucalyptus polyanthemus*) including a semi-mature tree and five much smaller trees. The small trees are coppice regrowth from the underground portions of lignotubers left after the original sapling trees were removed, and have a multi-trunked appearance similar to mallee eucalypts. The ant

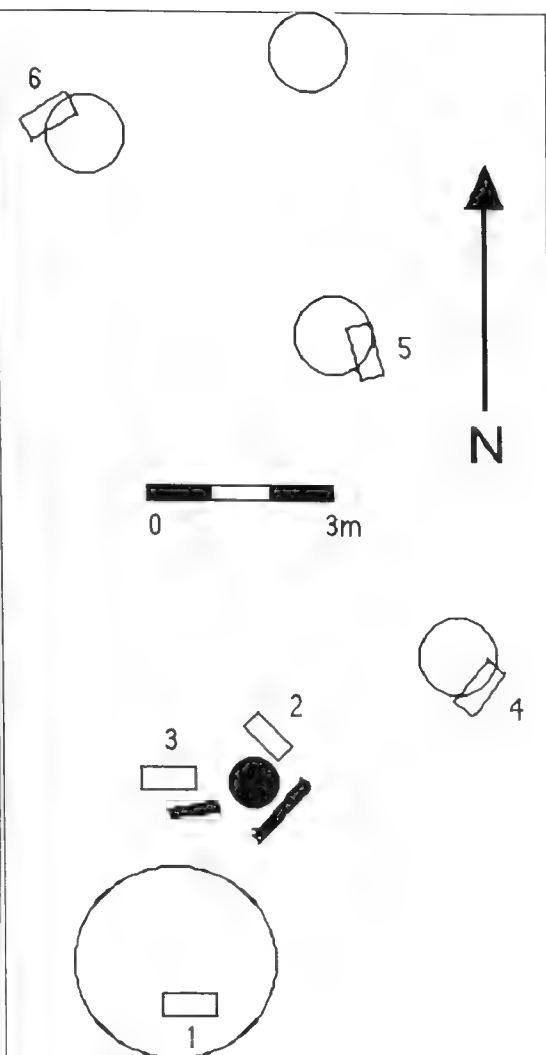


Figure 2. Placement of trap nests within the area occupied by *P. nitidus*. Open circles represent live eucalypts; the larger the circle, the greater the height and canopy width of the tree. Filled shapes represent dead wood on the ground, including the stump. Rectangles indicate trap nests, which are identified by numbers.

constructed byres of carton at the base of the coppice regrowth, as well as over the stump and other pieces of dead wood. The carton covering was conspicuous on the stump, and was the key factor in finding the colony.

This colony was only 20–25 m away from a pitfall grid operated fortnightly from February to July, 1994 (Miller, 1994). In spite of the proximity of this pitfall grid to the ant colony no individuals of *P. nitidus* were taken in pitfall samples, implying that the ant is restricted to the immediate area of the colony.

The ant colony was mostly underground; suitable nesting substrate above the ground was scarce. The extent of the subterranean colony could not be estimated. Ants were observed foraging on the eucalypts during daylight hours. The extent of nocturnal foraging was not established. Ants foraged in temperatures ranging from 15°C to over 37°C, although low temperature observations were not made. Foraging workers visited various honeydew-producing Homoptera, including female and nymphal Coccoidea, psyllid nymphs and eurytelid leaf-hoppers. These resources were not present in the area where Miller (1994) had a pitfall grid. Foraging did not seem to occur outside of the area colonised by the ants.

Most of the trap nests were colonised two days after being placed in the field (6 Jan 1995). Figure 3 indicates the presence of *A. myrmecophila* and *P. nitidus* in trap nests in the eastern colony during the study period. Trap nests 1, 4, 5 and 6 which were next to saplings all had workers entering the nests via the entrances, or through the crack between the two halves. Nest 3 which

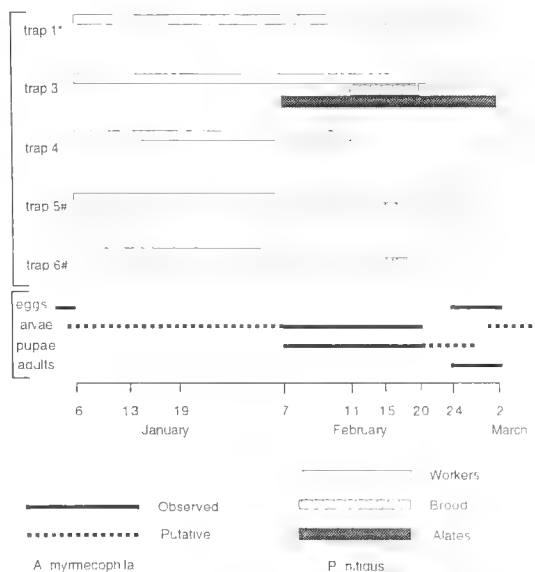


Figure 3. Presence of various life-history stages of *P. nitidus* and *A. myrmecophila* at Mount Piper, January–March, 1995. Large bars represent ant activity, lines represent butterfly activity. Trap nests 5 and 6 were the only trap nests to have *A. myrmecophila* larvae and pupae present. # indicates trap nests which had immature stages of *A. myrmecophila* present within or under them. * Trap 1 was adjacent to the eucalypt trunk with *A. myrmecophila* eggs.

was adjacent to the dead stump was colonised, but nest 2 which was also next to the stump was left unoccupied during the study period. The ants placed carton in the cracks between the two halves, in nest entrances not being used for access, and in the existing holes and cracks in the nest wood. The trap nests were left undisturbed for the first month, then were lifted so that ant activity under the nest could be observed. Nests 1 and 4 were largely abandoned after the initial colonisation (6 Jan 1995), but nests 3, 5 and 6 were very active for the duration of the study. Various quantities of ant brood (larvae, pupae and callows) were observed under nests 3, 5 and 6. Alate ants (winged sexual castes) were observed under nest 3, but were not found in any of the other nests. Trap nests 5 and 6 were the only nests observed to harbour immature stages of *Acrodipsas myrmecophila*.

Further searching during the 1994–1995 season resulted in the location of two additional colonies of *P. nitidus* in the Mount Piper region. Both colonies were larger than the eastern colony, and were located at the base of the mountain in open grassy regions to the west and south-west.

One colony was in open grassy woodland with mature grey box (*Eucalyptus microcarpa*), red stringybark (*E. macrorhyncha*) and *Acacia mearnsii*. A major component of this colony was in dead wood (stumps, branches and logs), indicating that the colony was larger above ground than the eastern colony. This colony was located on 16 Dec 1994, and was revisited 28 Dec 1994.

The other colony was in open *Themeda triandra* grassland with sapling and mature age *A. mearnsii* and sapling or suckering Red Box (*E. polyanthemus*). This colony resembled the eastern colony in that it had only a few small stumps occupied by the ant, with above-ground nesting activity largely confined to carton around the base of saplings. The area occupied by the colony was much larger than either of the other two colonies, but colony size was difficult to estimate as there were many small satellite colonies present on the edges of the main population. The colony is bounded by a shallow gully on the northern edge. This gully would become too wet during winter for ants to establish permanent colonies. This colony was located 23 Jan 1995.

Each colony was searched for immature stages of *Acrodipsas* spp. No evidence of either butterfly species was detected at these colonies.

Discussion

The location of *Papyrius nitidus* colonies and a breeding colony of *Acrodipsas myrmecophila* in the Mount Piper region is a major step forward in the determination of critical habitat for the butterfly and the ant. Predictions of suitable habitat (Beardsell, 1994) proved to be appropriate, with colonies found on well-drained gentle slopes in open, partially wooded regions. One element of the search strategy proved to be misleading. Previous records of immature stages of *A. myrmecophila* at historic localities have been associated with ant colonies in dead wood, (e.g., dead *Acacia pycnantha* at Ocean Grove). Ants in the eastern colony at Mount Piper were predominantly underground and around the base of living trees, and were inconspicuous. This situation has changed now that trap nests have been placed in the field within the eastern colony. Other requirements for suitable habitat based on observations of the ant at Mount Piper (Britton, 1995) and Cottles Bridge (Beardsell, 1994), would seem to be the presence of suitable foraging habitat, such as saplings and suckers of *Acacia* and *Eucalyptus* spp. which support populations of homopterans.

A major finding arising from our work at Mount Piper is that despite three detailed surveys over the three previous summers neither the colonies of the attendant ant (*Papyrius nitidus*) or immature stages of butterfly were located at Mount Piper until this survey. This strongly implies that long term studies are required to determine critical habitat of *A. myrmecophila* at any particular locality.

The refinement of searches for these invertebrates is a long-term process. Areas that had been thoroughly inspected and sampled in previous studies had populations of the ant. The biology of *P. nitidus* may influence the probability of locating new colonies. The ant is only active during the warmer part of the year (September to April), and on warm winter days, so winter searches may not be successful. The ant rarely forages outside of the colony area, so is not readily sampled by pitfall traps. The ant often moves between underground and surface parts of its nest.

However, once colonies are located, trap nests can be placed to increase ant habitat, and provide a method for assessing the presence or absence of *A. myrmecophila*. Trap nests are considered to be of critical importance in furthering the conservation management of this butterfly

species. In addition to the above points, trap nests could be used to "seed" new habitat with the ant, to provide a captive population of the butterfly with food and to re-introduce the butterfly into areas where the ant is already present. Trap nests may allow researchers to make detailed field-based observations of the ant/butterfly biology.

Further research into the biology and ecology of *P. nitidus* is needed. The phenology of the ant and the age that colonies attain is not known. Additional monitoring of Mount Piper colonies may determine whether colonies die out and recolonise over short periods of time. The eastern colony may be recently established, as this area has been thoroughly but unsuccessfully searched in previous studies (Britton and New, 1992, 1993; New et al., 1994; Beardsell, 1994; Miller, 1994). This colony may have been established only within the last year or so. The ant colonies west and south-west need further work to determine the presence or absence of breeding colonies of *Acrodipsas* spp. Trap nests, particularly in the west where there is a dearth of dead wood within the colony, may be the appropriate way both to increase ant populations and locate immature stages of the butterfly.

Conservation of *A. myrmecophila* is primarily dependent upon conservation of *P. nitidus*. Further research must focus on the ecology and life-history of *P. nitidus*, and the use of trap nests may prove to be essential in gaining new information.

Acknowledgments

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References

- Beardsell, C., 1994. *Report on field surveys from 22 October to 23 January 1994 for the Small and Large Ant-blue butterflies and their attendant ant species*. Unpublished report, Department of Conservation and Natural Resources.
- Britton, D.R., 1995. *Research on the ecology of the Coconut Ant and breeding biology of the Small and Large Ant-blue and other target butterflies at Mount Piper, Broadford, 1994/95*. Unpublished report for the Department of Conservation and Natural Resources.
- Britton, D.R. and New, T.R., 1992. *Ecology of the butterfly and ant community at Mount Piper, Victoria*. Unpublished report for the Department of Conservation and Environment.
- Britton, D.R. and New, T.R., 1993. *Communities of diurnal Lepidoptera in central Victoria, with emphasis on the Mt. Piper region, Broadford*. Unpublished report for the Department of Conservation and Natural Resources.
- Britton, D.R., New, T.R. and Jelinek, A., 1995. Rare Lepidoptera at Mount Piper, Victoria — the role of a threatened butterfly community in advancing understanding of insect conservation. *Journal of the Lepidopterists' Society* 49: 97–113.
- Common, I.F.B. and Waterhouse, D.F., 1981. *Butterflies of Australia*. Angus and Robertson: Australia.
- Dunn, K.L. and Dunn, L.E., 1991. *Review of the Australian butterflies*. Privately published, Melbourne.
- Hinkley, S., 1993. *The ant fauna of Mt. Piper: an investigation of factors affecting ant species richness and distribution and the effectiveness of pitfall trapping*. Unpublished Honours thesis, La Trobe University.
- Jelinek, A., 1991. Butterfly Community No. 1. *Flora and Fauna Guarantee Action Statement No. 6*. Department of Conservation and Environment, Victoria.
- Jelinek, A., 1992. *A recovery plan, research phase, for a threatened butterfly community at Mt. Piper in central Victoria*. Unpublished report to the Australian National Parks and Wildlife Service, Canberra.
- Miller, L., 1994. *Ant abundance and distribution on remnant native grasslands of Mt. Piper, Victoria*. Unpublished Honours thesis, La Trobe University.
- New, T.R., Britton, D.R. and Hinkley, S., 1994. *Recovery plan, research phase, for a rare and threatened butterfly community*. Report for 1993/94 for Department of Conservation and Natural Resources. Unpublished report, Department of Conservation and Natural Resources.
- New, T.R., Britton, D.R., Hinkley, S. and Miller, L. (in press) The ant fauna of Mount Piper, Broadford, and its relevance to environmental assessment and the conservation of a threatened invertebrate

- community. *Technical Report, Arthur Rylah Institute for Environmental Research.*
- Samson, P.R., 1989. Morphology and biology of *Acrodipsas illidgei* (Waterhouse and Lyell), a myrmecophagous lycaenid (Lepidoptera: Lycaenidae: Theclinae). *Journal of the Australian Entomological Society* 28: 161–168.

THE *OGYRIS IDMO* HEWITSON COMPLEX (LEPIDOPTERA: LYCAENIDAE) AS FLAGSHIP SPECIES FOR CONSERVATION IN SOUTHERN AUSTRALIA

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Abstract

Field, R.P., 1997. The *Ogyris idmo* Hewitson complex (Lepidoptera: Lycaenidae) as flagship species for conservation in southern Australia. *Memoirs of the Museum of Victoria* 56(2): 389-392.

The *Ogyris idmo* Hewitson complex consists of at least two large and spectacular butterflies only one of which is named. *O. idmo* is rare but widespread in the south-western corner of Western Australia and extremely rare in south-western Victoria and southern South Australia. Another undescribed rare species is currently known only from small areas near Kalgoorlie, Western Australia, Waikerie, South Australia and Ouyen, Victoria. All populations of both species are closely associated with one, or possibly two species of ants from the *Camponotus* 'myoporus' Clark group. Unlike other species of *Ogyris*, the larvae do not feed on mistletoes or other parasitic plants. There is evidence to suggest that for both species the eggs are deposited in or near the entrance to the ant nest, and the entire larval stage of the butterfly is completed within the nest, possibly as a predator of immature ants. There have been no confirmed records of *O. idmo* outside WA in over 40 years. The populations of the undescribed species are extremely small and/or vulnerable, that near Kalgoorlie being in a high-use recreation area, the population near Waikerie is in a roadside remnant of mallee vegetation surrounded by intensive agriculture and the recently discovered population near Ouyen is in a park reserve. Museum records indicate that the undescribed species also occurred at Broken Hill in New South Wales and at Mildura in Vic. The broad distribution of both species suggests that suitable habitat still exists for their continued survival. However, little is known about the biology of the butterfly and the intricate association it has with *Camponotus* ants. Studies on the ecology and distribution of these butterflies need to be undertaken so that their future survival can be assured. These species make ideal flagship species for conservation efforts in arid and semi-arid areas across southern Australia.

Introduction

The genus *Ogyris* Westwood, commonly called azures, contains some of the largest and most brilliantly coloured butterflies of the family Lycaenidae and yet their elusive nature has meant that they are seldom seen by the general public. McCubbin (1971), suggested that fewer than 1 person in 10,000 has ever seen a live *Ogyris* adult, although some species are not uncommon close to Perth, Adelaide, Melbourne, Sydney, and Brisbane. There are 15 named species in the genus, 12 occur in Australia and the other 3 are found in Papua New Guinea (Common and Waterhouse, 1981). Of the Australian species, the larvae of 10 are known to feed on mistletoes, often growing high in the tree tops. The butterflies usually fly close to their food plant and are therefore not often observed. Of the other 2 Australian species, one also feeds on parasitic plants, *Choretrum glomeratum* R. Br. and *Leptomeria preissiana* (Miq.) A. DC., both bushy root parasites. The remaining species, *Ogyris idmo* Hewitson, is the largest

and rarest species in the genus and the second largest lycaenid in Australia. The life history of this species is unknown, yet it is believed not to feed on parasitic plants (Common and Waterhouse, 1981).

As with most species of Lycaenidae, all the *Ogyris* have a strong association with ants. Of the 11 Australian species where the life history is known, this association is symbiotic, with the larvae and pupae of the butterfly presumably obtaining some protection from predators and parasites, while the ants obtain sugar secretions harvested from abdominal glands on the immature stages (Common and Waterhouse, 1981). In many cases the larvae live in the ants' nest, often at the base of the tree bearing the mistletoe and emerge at night, with ants in attendance to search for food. Pupation often occurs in the ants' nest, usually close to the entrance where escape by the butterfly is less hazardous. For *O. idmo*, the life history is largely unknown although the species is thought to be univoltine with the eggs being laid into nests of ants from the *Camponotus* 'myoporus' Clark group during

November. The larvae are thought to be predatory on immature ants (Common and Waterhouse, 1981). An unnamed species of *Ogyris* closely resembling *O. idmo*, occurs near Kalgoorlie, Western Australia, near Waikerie in South Australia and near Ouyen in Victoria. This species is also associated with ants from the *Camponotus* 'myoporus' group, but possible a different species from that associated with *O. idmo*. This butterfly seems to be bivoltine with flight periods in the spring and autumn. The eggs are laid on bark close to the ground at the entrance to the ants' nest.

Distribution of the *O. idmo* complex

Two subspecies of *O. idmo* are recognised (Common and Waterhouse, 1981; Dunn and Dunn, 1991). *O. i. idmo* Hewitson occurs in south-western WA, from Cape Arid National Park (east of Esperance), the Stirling Ranges, Windy Harbour (R. Hay pers. comm.), near Perth, and recently at Port Denison 300 km N of Perth (Williams et al., 1995). *O. idmo halmaturia* Tepper is known from western Vic. and southern SA, including Kangaroo Island. Nowhere is the species abundant and there are no museum records of *O. idmo* outside WA in over the last 40 years. However, in recent years the species has been locally common near Perth and at Mt Ragged in Cape Arid National Park (Field, 1987, 1990). The population at Cape Arid National Park is morphologically distinct from the typical ssp. *idmo* (Field, 1990) and the northern population (Port Denison) is intermediate in appearance between the typical populations from near Perth and that from Cape Arid National Park (Williams et al., 1995). Figure 1 shows the known distribution of *O. idmo* and locations with similar climates derived using CLIMEX (Sutherst and Maywald, 1985) based on a 0.65 match of climate (temperature maximum and minimum and rainfall pattern and total) to Esperance, WA. Locations with climates similar to Esperance mirror closely the known distribution of *O. idmo*, including the recent range extension of the species to Port Denison, 300 km N of Perth.

In WA, the undescribed *Ogyris* sp. is known only from near Kalgoorlie, over a few square kilometres to the north-east of Lake Douglas. This same species occurs locally at Ramco, near Waikerie in SA and from near Ouyen, Vic. and was recorded from Mildura, Vic. in October 1972 (B. Vardy collection) and from Broken, Hill, NSW in December 1912 (Museum of Victoria). The CLIMEX prediction for the species

based on a 0.7 climate match with Kalgoorlie includes large inland areas of south-western NSW, inland south-eastern SA and inland south-eastern WA (Figure 2).



Figure 1. Known distribution of *Ogyris idmo* (enclosed regions) and locations with climate matches (I) using CLIMEX (CSIRO) of at least 0.65 with Esperance (o). The largest dots have the closest climate match with Esperance and represent locations with the highest probability of finding populations of *O. idmo*.



Figure 2. Known distribution of *Ogyris* sp. (enclosed regions) and locations with climate matches (I) using CLIMEX (CSIRO) of at least 0.7 with Kalgoorlie (o). The largest dots have the closest climate match with Kalgoorlie and represent locations with the highest probability of finding populations of *Ogyris* sp.

Conservation status of the *O. idmo* complex

Although rare, *O. i. idmo* is widespread in south-western WA and occurs in a variety of habitats. Many of the sites where locally abundant populations occur are disturbed sites (Table 1). The disturbance, either through fire or some minor physical disruption of the soil, appears to favour the survival of the ant species on which the butterflies depend. At Mt Ragged an intense fire during February 1991 destroyed all above ground vegetation, however, this bright blue form (females only) of *O. i. idmo* was extremely abundant the following October (confirming that the immature stages are subterranean) and again quite rare in October 1993 and 1994. The butterflies appear to be widespread in Cape Arid National Park and at times are abundant near Mt Ragged. Specimens of this form are also known from near Scadden, 150 km to the west. The more western populations of *O. i. idmo* often occur near urban areas, plantation forests, easements and in recently burnt areas. The species also occurs in reserves such as the Stirling Ranges National Park where fire is the most influential environmental process.

The populations of *O. i. halmaturia* from South Australia and Victoria may all be extinct largely as a result of land clearing. No confirmed records from Vic. have been made since 1945

(Table 1) although many early records (Nov 1939) were adjacent to the Little Desert National Park where the dependent ant still exists. Kangaroo I. may offer the best chance of rediscovering the butterfly in SA. The ant is still abundant on the island both inside and outside the conservation parks. Kangaroo I. is also a major stronghold for the rare *Ogyris otares* C. and R. Felder (Fisher, 1978), a species that feeds on *Choretrum glomeratum*. *O. otares* has the same attendant *Camponotus* species that is associated with *O. idmo* and at at least one location in WA the two species of butterflies are sympatric (Williams et al., 1995).

The undescribed *Ogyris* species occurring at Lake Douglas, near Kalgoorlie, is only known from an area of a few square kilometres. The colony occurs within a public recreation area that can be subjected to significant human interference with numerous vehicle tracks crossing the main breeding areas. In some years since its first discovery in the early 1980s, the butterflies have been common but few specimens have been seen since 1991. This species also occurs in a small remnant roadside strip of mallee vegetation near Waikerie in SA. This site is surrounded by citrus orchards and vineyards that are subject to pesticide sprays that coincide with the flight periods of the butterfly. The butterflies at this site also tend to fly commonly in the

Table 1. Conservation status of the *Ogyris idmo* complex

Taxon	Location	Last captures	Status	Disturbance
<i>O. i. idmo</i>	Darling Range (near Perth) WA	1994	rare	Urban development/Forestry/Fire
	Port Denison	1994	rare	Township development
	Cape Arid NP WA	1994	rare (secure)	Fire
<i>O. i. halmaturia</i>	Kangaroo Is. SA	1934	extinct	Fire
	SA mainland	1951	vulnerable	Agriculture
	Kiata Vic	1945	extinct	Fire/Agriculture
"Kalgoorlie" <i>Ogyris</i> sp	Lake Douglas WA	1993	rare	Recreation
"Waikerie" <i>Ogyris</i> sp	Ramco SA	1996	vulnerable	Agriculture
	Ouyen Vic	1996	unknown (secure)	unknown (site in park reserve)
	Mildura Vic	1972	endangered	Grave digging
	Broken Hill NSW	1912	extinct?	

adjoining farmland as well as in the breeding area. Until 1996 the only confirmed Victorian site for this species was adjacent to the Mildura cemetery. Specimens had been caught in October of 1972, the season prior to several seasons of extensive flooding from the Murray River which inundated the site and may have caused the demise of the population. The ants are still very abundant at the site so that recolonisation by the butterflies, either naturally or by artificial reintroduction is a distinct possibility. However, two specimens were taken during February and April 1996 near the Pink Lakes, west of Ouyen where the attendant ants were in high numbers over large areas containing open mallee vegetation. It was at this site in April 1975 that Charles McCubbin (personal communication) had observed several specimens flying that were thought to have been *O. idmo halmaturia*. Given the time of the year, these specimens were undoubtedly the undescribed *Ogyris* sp. A single specimen from Broken Hill in the Museum of Victoria (Dunn and Dunn, 1991) is also thought to belong to this species but the precise location of the site is unknown.

The rare and possibly predatory nature of the species in the *Ogyris idmo* complex has provided a fascination amongst lepidopterists for many years. The unusual association with ants that exists with the complex provides an opportunity to highlight this interaction in broader conservation programs. The complex and the ants could thus be used as flagship species in the advocacy of conservation of biodiversity in areas where the complex exists now, potentially may occur, or has occurred in the past. It is important that the ecology of these species is elucidated as soon as possible so that a greater

understanding of the influence of disturbance can be predicted.

Acknowledgments

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References

- Common, I.F.B. and Waterhouse, D.F., 1981. *Butterflies of Australia*. Angus and Robertson: London. x + 682 pp.
- Dunn, K.L. and Dunn, L.E., 1991. *Review of Australian butterflies: distribution, life history and taxonomy. Part 3: Family Lycaenidae*. Published by the authors: Melbourne.
- Field, R.P., 1987. Notes on butterflies collected in south-west Western Australia, September-October, 1987. *Victorian Entomologist* 17(6):111-114.
- Field, R.P., 1990. Range extensions and the biology of some Western Australia butterflies. *Victorian Entomologist* 20(4): 76-82.
- Fisher, R.H., 1978. *Butterflies of South Australia*. Government Printer: South Australia. 272 pp.
- McCubbin, C., 1971. *Australian butterflies*. Thomas Nelson. 206 pp.
- Sutherst, R.W. and Maywald G.F., 1985. A computerised system for matching climates in ecology. *Agriculture, Ecosystems and Environment* 13: 281-299.
- Williams, M.R., Williams, A.E., Lundstrum, T.D., Hay, R.W., Bollam, H.H. and Graham, A.J., 1995. Range extensions and natural history notes for some Western Australian butterflies. *Victorian Entomologist* 25(5): 94-96.

BIODIVERSITY OF PLANTHOPPERS (HEMIPTERA: DELPHACIDAE) ON THE HAWAIIAN SILVERSWORD ALLIANCE: EFFECTS OF HOST PLANT PHYLOGENY AND HYBRIDISATION

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Abstract

Roderick, G.K. and Metz, E.C., 1997. Biodiversity of planthoppers (Hemiptera: Delphacidae) on the Hawaiian silversword alliance: effects of host plant phylogeny and hybridisation. *Memoirs of the Museum of Victoria* 56(2): 393–399.

Many hypotheses have been advanced to account for the biodiversity of herbivorous insects. Here we test whether the diversity of a group of planthoppers, genus *Nesosydne* (Hemiptera: Delphacidae), can be explained by the history and patterns of hybridisation of their host plants in the Hawaiian silversword alliance, many of which are critically endangered or threatened. Molecular data (DNA sequences of mitochondrial cytochrome oxidase I) for planthoppers examined to date reveals significant co-speciation between these insects and their hosts. *Nesosydne* planthoppers are highly host specific with each species feeding on only one plant species or on closely related species that hybridise. There was no evidence to support the “hybrid-bridge” hypothesis as a mechanism by which herbivorous insects may switch hosts. Nor was there evidence that plant hybrid zones were centres of insect biodiversity. Rather, patterns of host plant use within plant hybrid zones suggests that planthopper diversification follows host plant diversification.

Introduction

The current threats to biological diversity have necessitated the understanding of the forces responsible for both its generation and demise (Wilson, 1988; 1996). Insects are among the most diverse organisms, with over 1 million described to date and perhaps another 10 to 30 million remaining to be discovered in tropical regions (Erwin, 1982; 1986). Herbivorous species form a major component of these insects (Strong et al., 1984) and most explanations for their diversity are linked to the diversity of plants on which they feed (Mitter et al., 1988; 1991; Farrell and Mitter, 1993; Thompson, 1994; Funk et al., 1995; Futuyma et al., 1995).

Much of the current insect biodiversity was present even before the radiation of the flowering plants (angiosperms) and appears to be coincident with the earlier diversification of seed plants (Labandeira and Sepkoski, 1993). Herbivorous insects may have further diversified with the radiation of angiosperms which required pollinators (Ehrlich and Raven, 1964); indeed, some radiations of insect species do appear to be correlated with those of flowering plants (Mitter et al., 1988; 1991). Insect lineages

at the generic and family levels appear to be largely conservative with respect to their host affiliations and many species in these lineages are highly host specific (Dethier, 1954; Ehrlich and Raven, 1964; Farrell and Mitter, 1993). Current patterns of host plant use by herbivorous insects can be explained by one of two hypotheses, both of which can lead to greater herbivore diversity: co-speciation with host plants and host plant switching. Co-speciation is the matching of speciation events in two lineages, such that the two phylogenies resemble one another (see Brooks, 1979; Mitter and Brooks, 1983; Brooks, 1988; Hafner et al., 1994; Page, 1995a). Co-speciation may be a consequence of co-evolution, but may also arise through other mechanisms. By contrast, host-plant switching is a change of hosts (see Futuyma, 1983a; 1983b; Thompson, 1994) other than would be predicted by the host phylogeny, such that the two phylogenies are no longer congruent. Compilations of research on herbivorous insects and their hosts indicates that while a few insect radiations do appear to be tightly correlated with radiations of their hosts, most insect radiations show evidence of host-switching (Mitter et al., 1988; 1991; Farrell and Mitter, 1993; Funk et al., 1995).

Recently, it has been suggested that the frequent occurrence of hybrids between plant species may form centres of biodiversity or otherwise play a role in herbivore diversification (Floate and Whitham, 1993; Strauss, 1994; Whitham et al., 1994). Hybridisation between host species may also play a role in parasite diversification. Hybrid hosts not only create new niches, but may allow specialised parasites an escape from evolutionary dead ends (see Moran, 1988) — hybrids may provide a “bridge” to novel host species (Floate and Whitham, 1993). Whether “hybrid-bridges” are important in explaining the history and patterns of host plant use by herbivorous insects remains controversial (see Floate and Whitham, 1993).

The *Nesosydne* planthoppers (Homoptera: Delphacidae) in Hawaii are one of several insect radiations with members associated with the Hawaiian silversword alliance (Asteraceae) (see Roderick, in press). Here, we investigate factors underlying the biodiversity of these sap-feeding insects in light of the history and hybridisation of their plant hosts. We first test for the importance of “hybrid-bridges” by comparing phylogenetic histories of silversword plants and planthoppers. Secondly, we examine whether plant hybrid zones are centres for biodiversity, by examining planthopper species diversity across five hybrid zones.

Methods

Silversword Alliance.

The silversword alliance in Hawaii comprises 28 species, presumably with one common ancestor (Baldwin et al., 1991; Baldwin and Robichaux, 1995; Baldwin, in press). This radiation is among the most well-studied of all plant lineages in Hawaii (see Wagner and Funk, 1995) with published works on ecology, physiology, systematics, conservation status, and hybridisation (Carr, 1987). Carr (1985; 1990a; 1990b) has investigated the extent of hybridisation between members of the silversword alliance and has documented that many, if not most, members of the silversword alliance form natural hybrids in the field. Hybrid zones differ in:

1. the plant species involved,
2. the relatedness of plant species that hybridise,
3. the range of ecological conditions occupied, and
4. the extent of overlap between the hybrids and one or both parental species. Hybrids and potential F¹s have been identified by leaf size

and shape (Carr, 1985), and recently by genetic data (RAPDs, V. Caraway and C. Morden, unpubl. data; Friar et al., 1996).

Recently, Baldwin and colleagues (Baldwin et al., 1991; Baldwin and Robichaux, 1995; Baldwin, in press) have used molecular genetic data to generate a hypothesis of evolutionary relationships among members of the alliance (fig. 1). The alliance appears to be monophyletic and to contain distinct clades within Hawaii. Divergence among extant species is likely in the range of 4–6 MY, or no older than the age of Kauai (Baldwin and Robichaux, 1995; Baldwin, in press). Conflicting evidence from nuclear, karyotype, and cytoplasmic DNA data suggests that some species may be of hybrid origin. The existence of a phylogenetic hypothesis for plant species in the silversword alliance is an essential element in the analysis presented here for several reasons:

1. it provides the basis for tests of co-speciation of planthoppers and their host plants,
2. it gives insight into the degree of host specificity, and
3. it establishes the relatedness between parental plant species associated with each plant hybrid zone.

Nesosydne planthoppers

Many radiations of insects, including delphacid planthoppers, are endemic to Hawaii (Simon, 1987; Howarth and Mull, 1992; Asquith, 1995; Eldredge and Miller, 1995; Miller and Eldredge, 1996). In contrast to other delphacid planthoppers which are mainly grass feeders (Denno and Roderick, 1990; Denno et al., 1991; Roderick, 1994), these planthoppers in Hawaii feed on a wide variety of plant families (Zimmerman, 1948; Swezey, 1954). The genus *Nesosydne* in Hawaii contains at least 80 species (Zimmerman, 1948). Systematic studies of the genus *Nesosydne* based on morphological characters are in progress (Asche, in press). *Nesosydne* is now thought to be polyphyletic and represent several independent colonisations of Hawaii with subsequent radiations within the archipelago (M. Asche, personal communication). At least 15 *Nesosydne* species are reported to be found only on plant species in the Hawaiian silversword alliance (Zimmerman, 1948; Swezey, 1954); whether these species form a monophyletic group within the *Nesosydne* has not been established based on morphological characters, although the molecular data presented here support monophyly. Presently, no other literature exists on abundance, life stages,

and seasonality of *Nesosydne* planthoppers on these different host plant species.

Host plants associations

Planthoppers were collected using an aspirator and sweeping on members of the silversword alliance including five extensive hybrid zones (see fig. 1). For these collections, R. Robichaux provided information on the likelihood that individual plants were hybrids, although in each hybrid zone there is a continuum of backcrosses between likely parental species. Insects were frozen at -80°C shortly after collection.

Planthopper history

A 441 base pair piece of cytochrome oxidase I was amplified using primers C1-J-1751 'Ron' and C1-N-2191 'Nancy' (designed by R. Harrison lab, Simon et al., 1994) To date, we have examined individuals in six *Nesosydne* species. The frequency of transitions and transversions was examined for *Nesosydne* species using several genetic distances: uncorrected pairwise percent divergence, Kimura (1980) 2-parameter, and Tamura-Nei (1993). A phylogeny was reconstructed using both parsimony (PAUP, Swofford, 1993) and neighbor-joining (Phylip, Felsenstein, 1993; MEGA, Kumar et

A. Silversword Alliance

B. *Nesosydne* Planthoppers

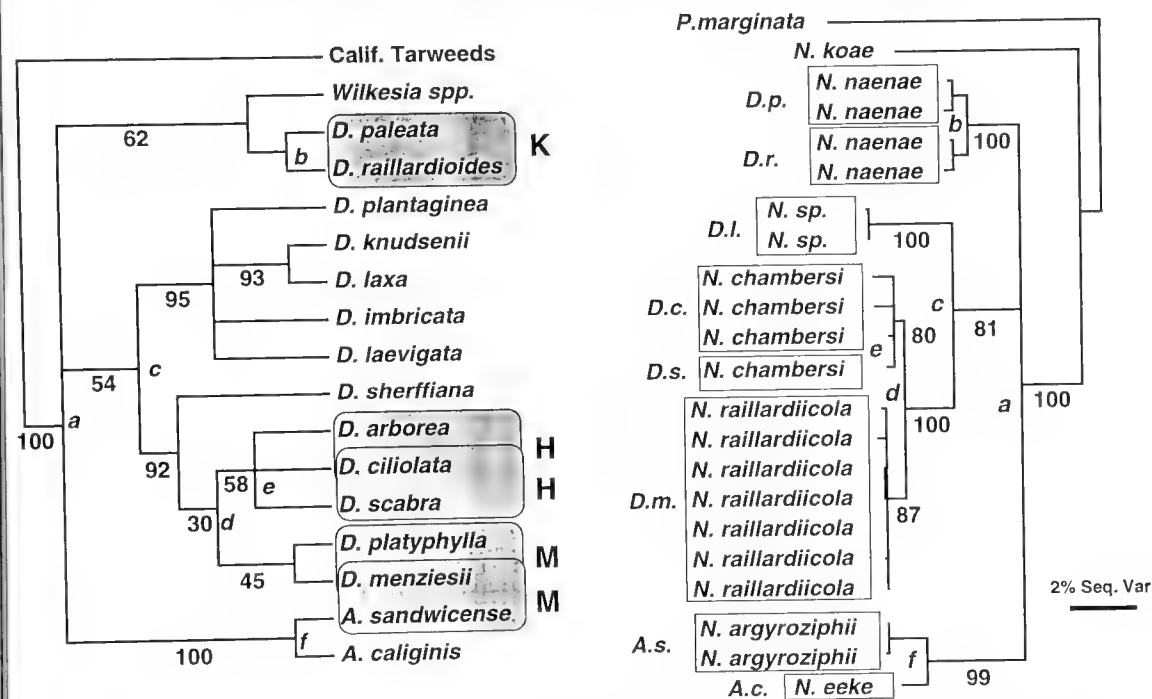


Figure 1. A. Phylogenetic hypothesis of evolutionary relationships among selected plant species in the Hawaiian silversword alliance showing major clades (after Baldwin and Robichaux, 1995). The total number of species in the radiation is 28 (not all shown), which likely evolved from a single California tarweed species only in the past 4–6 million years (Baldwin, in press). Hybrid zones between pairs of taxa examined in the current study are shown by shaded boxes with islands noted to the right (K = Kauai, M = Maui, H = Hawaii). Bootstrap support (%) for particular clades are shown below branches. B. Phylogenetic reconstruction by parsimony of the history of *Nesosydne* species found on members of the Hawaiian silversword alliance using DNA sequence variation in mtDNA COI. Branch lengths are proportional to sequence variation. Numbers below branches denote bootstrap support (%) for nodes. Multiple individuals of the same species are shown with the same name. Boxes show host plant affiliations, with names to the left. On both reconstructions, points corresponding to co-speciation between planthoppers and their host plants are lettered a–f.

al., 1993). Bootstrapping ($n=500$) was used to provide a level of confidence associated with each branch. Outgroups included another Hawaiian *Nesosydne* planthopper, *N. koae*, which feeds on *Acacia koa* (see O'Connell, 1991) and *Prokelisia marginata*, a delphacid from the continental United States (see Roderick, 1987; Denno et al., in press).

Tests of hypotheses for herbivore diversity

The hybrid-bridge hypothesis predicts that host switching has occurred in the history of relationships between plants and their hosts. To test this hypothesis, the phylogeny of the planthoppers was compared to that of the silversword alliance. The planthopper phylogeny was mapped onto Baldwin and Robichaux's (1995) phylogeny for the silversword alliance based on sequences of nuclear ribosomal DNA. Events of hybrid switching and co-speciation, were reconstructed using TreeMap (Page, 1995b). A randomisation test (by "randomising" the planthopper tree using TreeMap, Page, 1995b) was used to test significance of the observed level of co-speciation between planthoppers and their plant hosts.

To test of whether plant hybrid zones are centres for insect diversity, the number of planthopper species was examined across five hybrid zones and compared to taxa and locations where hybridisation does not occur.

Results

Host plants associations

Nesosydne planthoppers have now been collected on 13 out of 28 members of the silversword alliance. Based on observations of both adults and developing nymphs, many earlier recorded associations are either spurious, site-specific, or no longer occur (Roderick, unpubl. data). On five plant species no planthoppers were found. On the other plant species, only one planthopper species occurred in sympatry on the same host plant species. Where a planthopper species occurred on more than one host species, the hosts were closely related and/or hybridise. These host records indicate that planthopper species in this group are highly host-specific to either single plant species or closely related species.

Planthopper history

The 441 base pair piece of cytochrome oxidase I amplified was one codon insertion longer than *Drosophila yakuba* (Clary and Wolsten-

holme, 1985). Transitions were approximately double transversions for the range of genetic distances encompassing the *Nesosydne* planthoppers feeding on the silversword alliance and both transitions and transversions increased linearly over this range of genetic distances. The linear increase indicates that cytochrome oxidase I is a good candidate for the evolutionary relationships investigated here, and that both transitions and transversions contain useful information. If island age can be used as a rough time frame, these genetic distances correspond to approximately 2 percent per million years (for island ages see Carson and Clague, 1995). Parsimony, neighbor-joining, and maximum likelihood gave identical trees with similar bootstrap values; only the parsimony tree is shown here (fig. 1B). While there may be other species not examined here that would fall within those feeding on the silversword radiation, this group was supported by multiple synapomorphies that distinguished it significantly from *N. koae*. The time frame suggested here for the diversification of *Nesosydne* species that feed on the silversword alliance is consistent with a single origin of these insects in Hawaii and corresponds to the age of the silversword alliance.

Tests of hypotheses for herbivore diversity

The reconstruction of planthopper and host plant phylogenies resulted in 6 co-speciation events and no host-switching (fig. 1). It should be noted that the base of the tree for both host plants and planthoppers was unresolved. The randomisation test shows that this number of co-speciation events is significant ($p < 0.01$). Note that the method identifies a "co-speciation" events for the different planthopper haplotypes collected on *D. raillardoides* and *D. palcata*, and *D. ciliolata* and *D. scabra*, even though the planthoppers collected on each species pair are identified as the same species (see fig. 1B). The reconstructed co-phylogenies provide no evidence of recent host-switching. Research is ongoing to determine whether this pattern of co-speciation is supported when all species of Hawaiian *Nesosydne* are included.

The reconstructed co-phylogenies provide no evidence to suggest that host-switching is important in the host associations documented here, as would be predicted by the "hybrid-bridge" hypothesis.

Planthoppers were collected over 5 extensive hybrid zones (fig. 2). Baldwin and Robichaux's

Planthopper Use of Hybrids:

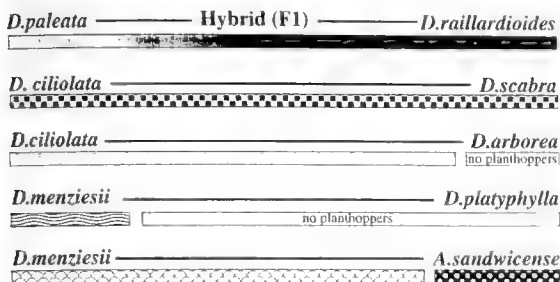


Figure 2. Patterns of planthopper host plant use and characteristics of five hybrid zones between members of the Hawaiian silversword alliance. Range of hybrid use for each planthopper species noted by shaded rectangles. In two hybrid zones, parental plant species were found with no planthoppers. See text for islands and degree of relatedness between plant taxa.

(1995) data provide information on the relatedness of the plant species involved in each of these hybrid zones. In two hybrid zones between closely related plant species a single planthopper species spanned each entire hybrid zone: *D. paleata* and *D. raillardoides* (Kauai) and *D. ciliolata* and *D. scabra* (Hawaii). In two other hybrid zones between close plant relatives, a single planthopper species was associated with only one parental plant species; in one of these, the planthopper also occurred on all identifiable hybrids while in the other, the planthopper's range was restricted to the parental species: *D. ciliolata* and *D. arborea* (Hawaii) and *D. menziesii* and *D. platyphylla* (Maui). On intergeneric hybrids between *A. sandwichense* and *D. menziesii* (Maui) both parental plant species supported one planthopper species each and all apparent hybrids shared the species associated with *D. menziesii*. No greater diversity of planthopper species was observed in these hybrid zones than on silversword taxa and locations where hybridisation does not occur: four of five hybrid zones supported only one planthopper species and one supported only two species. Thus, the evidence does not support the hypothesis that silversword hybrid zones are centres for planthopper biodiversity.

Discussion

The Hawaiian *Nesosydne* planthoppers are highly host specific, with each species feeding on one or a few closely related hosts. The significance of co-speciation demonstrates that species

of planthoppers and members of the silversword alliance examined to date share parallel or co-phylogenies. Unfortunately, this result does not identify the processes that underlie the pattern (see Farrell and Mitter, 1993; Funk et al., 1995; Price, 1996). For example, co-phylogenies may arise though a number of processes that may include vicariance on one or both players, co-evolution, or adaptation by one player in response to the other. It is possible that major vicariant events, such as island and volcano formation, have shaped both planthopper and plant phylogenies concurrently, and that planthopper adaptation to hosts may not be important in explaining significant co-speciation.

Some biological observations can shed light on this issue. Research on other delphacid planthoppers suggests that planthoppers can adapt to closely related novel hosts. For example, numerous studies have shown that the rice brown planthopper, *Nilaparvata lugens*, can overcome new "resistance genes" in rice in only a few generations, but that host-switching is limited (for review Roderick, 1994). Investigation of hybrid zones presented here demonstrate that the same planthopper species is not found on distantly related hosts, despite sympatry and the existence of intermediate hybrids. This pattern of host association indicates that limits exist to host adaptation by planthoppers. That single species feed on some closely related hosts but not on others suggests that some closely related plant species have not diverged sufficiently to limit planthopper distribution. These observations are consistent with the hypothesis that diversity of *Nesosydne* planthoppers parallels and likely follows the diversity generated in the silversword alliance.

Data presented here do not yet adequately address the role of hybridisation in the host species in causing differentiation of planthopper populations and species. For the taxa examined to date, hybrid bridges and host-switching do not explain current patterns of host use by planthoppers; patterns of host use can be predicted entirely on the basis of co-speciation of the planthoppers and hosts. Planthoppers are no more diverse in number of species than planthoppers; collected on non-hybrids. Whether genetic diversity within planthopper species is greater in hybrid zones remains to be tested. More rigorous tests for the role of plant hybridisation in the diversification of *Nesosydne* planthoppers are now underway and include reciprocal transplant studies, population genetic assessments of planthoppers across plant hybrid

zones, and a more complete molecular analysis of *Nesosydne* planthoppers on members of the silversword alliance and other host plants.

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References

- Asche, M., in press. Systematics and evolution of Hawaiian Fulgoroidea (Hemiptera). *Pacific Science*.
- Asquith, A., 1995. Evolution of Sarona (Heteroptera, Miridae). Pp. 90–120 in: Wagner, W.L. and Funk, V.A. (eds.), *Hawaiian biogeography*. Smithsonian Institution Press: Washington, D.C.
- Baldwin, B. and Robichaux, R., 1995. Historical biogeography and ecology of the Hawaiian silversword alliance (Compositae): new molecular phylogenetic perspectives. Pp. 259–287 in: Wagner, W. and Funk, V. (eds), *Hawaiian biogeography*. Smithsonian Institution Press: Washington, D.C.
- Baldwin, B.G., in press. Adaptive radiation of the Hawaiian silversword alliance: congruence and conflict of phylogenetic evidence from molecular and non-molecular investigations. In: Givnish, T. and Sytsma, K.J. (eds), *Molecular evolution and adaptive radiation*. Cambridge University Press: Cambridge.
- Baldwin, B.G., Kyhos, D.W., Dvorak, J. and Carr, G.D., 1991. Chloroplast DNA evidence for a North American origin of the Hawaiian silversword alliance (Asteraceae). *Proceedings of the National Academy of Sciences (USA)* 88: 1840–1843.
- Brooks, D.R., 1979. Testing the context and extent of host-parasite coevolution. *Systematic Zoology* 28: 299–307.
- Brooks, D.R., 1988. Macroevolutionary comparisons of host and parasite phylogenies. *Annual Review of Ecology and Systematics* 19: 235–259.
- Carr, G.D., 1985. Monograph of the Hawaiian Madinae (Asteraceae): *Argyroxiphium*, *Dubautia*, and *Wilkesia*. *Allertonia* 4: 1–123.
- Carr, G.D., 1987. Beggar's ticks and tarweeds: masters of adaptive radiation. *Trends in Ecology and Evolution* 2: 192–195.
- Carr, G.D., 1990a. 11. Asteraceae. 9. *Argyroxiphium* DC Silversword. Pp. 258–262 in: Wagner, W.L., Herbst, D.R. and Sohmer, S.H. (eds), *Manual of the flowering plants of Hawaii*. Vol. 1. University of Hawaii Press: Honolulu.
- Carr, G.D., 1990b. 11. Asteraceae. 26. *Dubautia* Gaud. Na'ena'c, kupaoa. Pp. 292–308 in: Wagner, W.L., Herbst, D.R. and Sohmer, S.H. (eds), *Manual of the flowering plants of Hawaii*. Vol. 1. University of Hawaii Press: Honolulu.
- Carson, H.L. and Clague, D.A., 1995. Geology and biogeography of the Hawaiian Islands. Pp. 14–29 in: Wagner, W.L. and Funk, V.A. (eds), *Hawaiian biogeography. Evolution on a hot spot archipelago*. Smithsonian Institution Press: Washington, D.C.
- Clary, D.O. and Wolstenholme, D.R., 1985. The mitochondrial DNA molecule of *Drosophila yakuba*: nucleotide sequence, gene organization, and genetic code. *Journal of Molecular Evolution* 22: 252–271.
- Denno, R.F. and Roderick, G.K., 1990. Population biology of planthoppers. *Annual Review of Entomology* 35: 489–520.
- Denno, R.F., Roderick, G.K., Olmstead, K. and Döbel, H.G., 1991. Density-related migration in planthoppers: the role of habitat persistence. *American Naturalist* 138: 1513–1541.
- Denno, R.F., Roderick, G.K., Peterson, M.A., Huberty, A.F., Döbel, H.G., Eubanks, M.D., Losey, J.E. and Langellotto, G.A., in press. Habitat persistence and dispersal in planthoppers. *Ecological Monographs*.
- Dethier, V.G., 1954. Evolution of feeding preferences in phytophagous insects. *Evolution* 8: 833–854.
- Ehrlich, P.R. and Raven, P.H., 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586–608.
- Eldredge, L.G. and Miller, S.E., 1995. How many species are there in Hawaii? *Bishop Museum Occasional Papers* 41: 3–18.
- Erwin, T.L., 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* 36: 74–75.
- Erwin, T.L., 1986. The tropical forest canopy: the heart of biotic diversity. Pp. 123–129 in: Wilson, E.O. (ed.), *Biodiversity*. National Academy of Sciences: Washington, D.C.
- Farrell, B.D. and Mitter, C., 1993. Phylogenetic determinants of insect/plant community diversity in: Ricklefs, R.E. and Schluter, D. (eds), *Species diversity in ecological communities*. University of Chicago Press: Chicago.
- Felsenstein, J., 1993. *Phylogeny*. University of Washington.

- Floate, K.D. and Whitham, T.G., 1993. The 'hybrid bridge' hypothesis: host shifting via plant hybrid swarms. *American Naturalist* 141: 651-662.
- Friar, E.A., Robichaux, R.H. and Mount, D.W., 1966. Molecular genetic diversity following a population crash in the Endangered Mauna Kea silversword, *Argyroxiphium sandwicense* spp. *sandwicense* (Asteraceae). *Molecular Ecology* 5: 687-691.
- Funk, D.J., Futuyma, D.J., Ort, G. and Meyer, A., 1995. A history of host associations and evolutionary diversification for Ophrellia (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. *Evolution* 49: 1008-1017.
- Futuyma, D.J., 1983a. Evolutionary interactions among herbivorous insects and plants. Pp. 207-231 in: Futuyma, D.J. and Slatkin, M. (eds.), *Coevolution*. Sinauer: Sunderland, Mass.
- Futuyma, D.J., 1983b. Selective factors in the evolution of host choice by phytophagous insects. Pp. 227-244 in: Ahmad, S. (ed.), *Herbivorous insects*. Academic Press: New York.
- Futuyma, D.J., Keese, M.C. and Funk, D.J., 1995. Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. *Evolution* 49: 797-809.
- Hafner, M.S., Sudman, P.D., Villablanca, F.X., Spradling, T.A., Demastes, J.W. and Nadler, S.A., 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science* 265: 1087-1090.
- Howarth, F.G. and Mull, W.P., 1992. *Hawaiian insects and their kin*. University of Hawaii Press: Honolulu.
- Kimura, M., 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111-120.
- Kumar, S., Tamura, K. and Nei, M., 1993. *MEGA: Molecular Evolutionary Genetic Analysis*. The Pennsylvania State University: University Park, PA.
- Labandeira, C.C. and Sepkoski, J.J., Jr., 1993. Insect diversity in the fossil record. *Science* 261: 310-315.
- Miller, S.E. and Eldredge, L.G., 1996. Numbers of Hawaiian species: supplement 1. *Bishop Museum Occasional Papers* 45: 8-17.
- Mitter, C. and Brooks, D.R., 1983. Phylogenetic aspects of co-evolution. In: Futuyma, D.J. and Slatkin, M. (eds.), *Coevolution*. Sinauer: Sunderland, Mass.
- Mitter, C., Farrell, B. and Futuyma, D.J., 1991. Phylogenetic studies of insect-plant interactions: insights into the genesis of diversity. *Trends in Ecology and Evolution* 6: 290-293.
- Mitter, C., Farrell, B. and Wiegmann, B., 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *American Naturalist* 132: 107-128.
- Moran, N., 1988. The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. *American Naturalist* 132: 681-706.
- O'Connell, C., 1991. *Acoustic communication and sexual selection in a group of Hawaiian planthoppers (Homoptera: Delphacidae)*. Masters thesis. University of Hawaii, Manoa.
- Page, R.D.M., 1995a. Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics* 10: 155-173.
- Page, R.D.M., 1995b. *TreeMap*. University of Oxford: Oxford.
- Price, P.W., 1996. *Biological evolution*. Saunders College Publishing: Fort Worth, Texas.
- Roderick, G.K., 1987. *Ecology and evolution of dispersal of a Pacific salt marsh insect*. Ph.D. thesis. University of California, Berkeley.
- Roderick, G.K., 1994. Genetics of host plant adaptation in delphacid planthoppers. Pp. 551-570 in: Denno, R.F. and Perfect, T.J. (eds.), *Planthoppers: their ecology and management*. Chapman and Hall: London.
- Roderick, G.K., in press. Herbivorous insects and the Hawaiian silversword alliance: co-evolution or co-speciation? *Pacific Science*.
- Simon, C., 1987. Hawaiian evolutionary biology: an introduction. *Trends in Ecology and Evolution* 2: 175-178.
- Simon, C., Fratti, F., Beckenbach, A., Crespi, B., Liu, H. and Flook, P., 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87: 651-701.
- Strauss, S., 1994. Levels of herbivory and parasitism in host hybrid zones. *Trends in Ecology and Evolution* 9: 209-214.
- Strong, D.R., Lawton, J.H. and Southwood, R., 1984. *Insects on plants*. Blackwell: Oxford.
- Swezey, O.H., 1954. *Forest entomology in Hawaii*. Bishop Museum: Honolulu.
- Swofford, D.L., 1993. *PAUP. Phylogenetic analysis using parsimony*. Sinauer: Sunderland, Mass.
- Tamura, K. and Nei, M., 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* 6: 447-459.
- Thompson, J.N., 1994. *The coevolutionary process*. The University of Chicago Press: Chicago.
- Wagner, W.L. and Funk, V., 1995. *Hawaiian biogeography: evolution on a hot spot archipelago*. Smithsonian Institution Press: Washington, D.C.
- Whitham, T.G., Morrow, P.A. and Potts, B.M., 1994. Plant hybrid zones as centers of biodiversity: the herbivore community of two endemic Tasmanian eucalypts. *Oecologia* 97: 481-490.
- Wilson, E.O., 1988. *Biodiversity*. National Academy Press: Washington, D.C.
- Wilson, E.O., 1996. Insects: the ultimately biodiverse animals. P. XVI in: *XX International Congress of Entomology Proceedings*. Firenze, Italy.
- Zimmerman, E.C., 1948. *Homoptera: Auchenorrhyncha*. University of Hawaii Press: Honolulu.

RANGE CONTRACTION AND EXTINCTION VULNERABILITY: WHAT IS NATURAL?

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Abstract

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The potential of species to generate new taxa or go extinct may be a consequence of their evolutionary history. Here, parameters involved in the natural contraction of species ranges, in particular whether distributional ranges have a phylogenetic component, and to what extent the pattern of distributional change is affected by the scale at which populations differentiate, are examined. It is argued that, for taxa in which local differentiation is impossible, the primary opportunity for taxonomic divergence will only occur subsequent to colonisation of a new habitat, at which time taxa are also likely to expand their geographic and ecological range. In such a scenario, the most ancestral species will be relictual, with the narrowest ranges and greatest vulnerability to extinction. For taxa in which local population subdivision is possible subsequent to colonisation of a land mass, subdivided taxa become progressively more restricted in geographic and ecological range. In this second scenario the more derived species will be confined to ever-decreasing ranges, their probability of extinction coincidentally enhanced. Representatives of various lineages from the Hawaiian Islands are used to test these concepts. First, for spiders in the genus *Tetragnatha*, the phylogeny of two clades that differ in vagility is compared. As predicted, more derived species have broader ranges in the more vagile clade. In the more sedentary clade, the more derived species appear to be more restricted. For flies in the genus *Drosophila*, and plants in the Hawaiian silversword alliance, genus *Dubautia* on Kauai, known molecular data sets were used to examine the history of species in terms of population size. Applying recent theory based on coalescence, it is shown that the *Drosophila* lineage has been expanding its range through its history, as expected from a group that requires colonisation of a new land mass to form new species. On the other hand, the *Dubautia* lineage has suffered range contraction through its history, which is also as predicted because the group differentiates extensively within the same mountain mass. The results provide a method with which to predict how species will respond to conservation action. This reasoning suggests that species that are confined to small ranges as a result solely of their phylogenetic legacy are unlikely to be vulnerable to immediate extinction. However, species that have been confined to small ranges as a result of recent ecological modification, such as alien invasion, are highly vulnerable to extinction.

Introduction

Anthropogenic disturbance, either direct or indirect, is causing species to decline much more rapidly than they can be replaced. No area in the United States has such a high proportion of endemic species nor suffers the impact from as many new species annually as Hawaii. As a consequence, the Hawaiian archipelago represents a microcosm for global issues and concerns for the generation and loss of biodiversity. Here, distributional range is used as an indicator of vulnerability to extinction. Natural parameters that may dictate changes in the distributional range of species are considered. Anthropogenic factors responsible for accelerating species range contraction and demise are then examined.

The natural propensity of species to go extinct

can be examined by considering the following two questions:

1. Do patterns of geographic and ecological range expansion and contraction have a phylogenetic component?
2. To what extent does the scale at which population subdivision occurs, affect patterns of distributional change.

Previous studies have suggested that the evolutionary course leading to extinction is at least somewhat deterministic and predictable (Ricklefs, 1990): Species tend to undergo regular changes in geographic and ecological range over evolutionary time, although the nature of the relationship remains unclear. Elucidation of the mechanisms of such a relationship could provide an answer to a critical question in the analysis of biodiversity: Which species are

naturally prone to extinction, and which might serve as a crucible for evolution and future speciation?

The most widely recognised patterns of geographic change during taxonomic diversification are those in which there is a progressive, largely irreversible shift towards habitat specialisation during speciation episodes (Darlington, 1957, 1959, 1971; Wilson, 1961; Erwin, 1985). Wilson's (1959, 1961) 'taxon cycle' was used to describe such changes in the distributional pattern of Melanesian ants. He suggested that widespread, dispersive populations give rise to many more restricted and specialised species. The related 'taxon pulse' hypothesis of Erwin (1979) provides a general explanation of patterns of lineage radiation and extinction in carabid beetles. Regular changes in ecological and geographical distribution have now been recognised in many island systems (e.g., Cox and Ricklefs, 1977; Ricklefs, 1990). A number of studies have attempted to test these regular changes in distribution, but have failed to produce conclusive results (e.g., Johnston, 1975; Ricklefs and Cox, 1972, 1978; Pregill and Olsen, 1981; Jones et al., 1987; Liebherr and Hajek, 1990). Part of the problem may be the difficulty in recognising and defining stages within a cycle of distributional change versus merely documenting patterns (Pregill and Olson, 1981). In addition, it is often unclear as to the scale on which the cycle should operate. Failure to detect a cycle may indicate that insufficient time has elapsed for a pattern to develop. Alternatively, the cycle may have run its course, and the pattern of distributions it generated may have been obliterated by subsequent extinctions and interactions.

The recent development of phylogenetic analysis allows the prediction and testing of different biogeographical, ecological, and behavioral phenomena against an evolutionary framework (see Harvey and Pagel, 1991; Maddison and Maddison, 1992 for recent reviews). Such analyses therefore present an opportunity to measure the role of evolution in dictating changes in geographic and ecological range. Liebherr and Hajek (1990) used a cladistic approach to test the reality and generality of regular changes in distributions through the phylogeny of a lineage. They examined eight groups of New World carabid beetles and compared cyclic changes in habitat preference to patterns of data generated randomly under a null hypothesis. Their results did not support the predicted unidirectional shifts towards specialisation in habitat occupation.

The abundant evidence for ecological release and range expansion during the initial establishment of species in new habitats, and subsequent increase in range fragmentation and restriction (MacArthur et al., 1972), indicates that cycles of distributional change are real phenomena for some, and perhaps most, species (Ricklefs, 1990). Hence, tendencies towards extinction have an evolutionary component that is potentially predictable. The reason for the lack of evidence for such directional shifts in ecological and geographic range when tested using phylogenetic methodology may be a consequence of different mechanisms and levels through which a regular cycle in distributional range could potentially be achieved:

Conditions eliciting different patterns of distributional change

1. Colonisation

Populations frequently initiate a cycle of distributional change upon colonisation of a novel habitat or an unoccupied set of niches, during which they undergo ecological release, and expand their range, adopting a more generalised habit (e.g., Cox and Ricklefs, 1977; Otto and Svenson, 1982). During this period of release, divergence can occur rapidly (Carson, 1968, 1982; Carson and Templeton, 1984).

2. Adaptation

Over time, a population tends to adapt to local environmental conditions and/or be competitively displaced from part of its original range by new colonists. Concomitantly, the population may become fragmented, and its distributional range may be reduced. However, the evolutionary context of population fragmentation and change in distributional range is likely to depend on the extent of interdemographic gene flow and/or local selection:

a Minimal local differentiation. When a population of colonists is vagile with weak habitat associations, then very little local differentiation is likely to occur (Slatkin, 1985, 1987). The population would be constrained from differentiating on a local scale, a situation reflected in Figure 1A. Over time, range fragmentation and competition from heterospecifics would restrict the range of the colonists, increasing their vulnerability to extinction. But individuals could go on to colonise new environments as they became available. A regular change in geographic and/or ecological distribution would be evident if differentiation occurred subsequent to

colonisation. The youngest species would have the most widespread ecological and geographic distribution, while the oldest would have the most fragmented and/or restricted distribution.

- b Considerable local differentiation.* If the population of colonists were more sedentary and/or had a stronger tendency to be associated with specific habitat types, then fragmented populations may differentiate due to local selection or genetic drift (Wright, 1951), and each isolate may become specialised to local conditions

(Rosenzweig, 1978, 1990; Wood, 1980; Bush and Howard, 1986; Wood and Keese, 1990). This situation is reflected in Figure 1B. Speciation would occur coincidentally with fragmentation of the initial population, and extinction probability would increase with each new taxon formed.

These different scenarios all suggest that phylogenetic affinity could play an important role in dictating geographic range, and hence vulnerability to extinction. However, the evolutionary causes and distributional consequences differ for each situation. Therefore, there may be contrasting patterns of phylogeny underlying similar present-day patterns of geographic and ecological range. Previous studies have shown that for more vagile taxa, where speciation would most likely be dictated by geographical separation, the most ancestral species appear to be the most specialised and have the smallest ranges, while the most derived species are more generalised and/or widespread (Mindell et al., 1989; Moran, 1988; Carson and Kaneshiro, 1976). Alternatively, in less vagile species, or those exhibiting a propensity towards fine scale ecological isolation, it is possible for divergence to occur between contiguous habitats. Examples of less vagile/ecologically specialised groups might include cave-dwelling spiders (Cesaroni et al., 1981), some beetles (Ball, 1985; Erwin, 1985; Howden, 1985) and ants (Wilson, 1961) and perhaps also some vertebrates (e.g., salamanders, Larson et al., 1981). In each of these cases, the derived species appear to be the more specialised and restricted.

Speciation (Gillespie, 1991 a, b, 1992a, 1993; Gillespie and Croom, 1995; Gillespie et al., 1994) and extinction (Gillespie, 1992b; Gillespie and Reimer, 1993) have recently been examined in a radiation of spiders in the long-jawed orb-weaving genus *Tetragnatha* in the Hawaiian Islands. The tetragnathid radiation spans a tremendous spectrum of morphologies, ecological affinities, and behaviors. One entire clade of 16 species ('spiny-leg' clade) has abandoned web building, with the concomitant adoption of a vagile, cursorial predatory strategy. A second clade ('elongate' clade) consists entirely of sedentary web-building species. In this study the Hawaiian *Tetragnatha* are used to examine distributional changes through phylogeny. The tendency of lineages to expand or contract their range during their evolutionary history is then tested using the methodology developed by Nee and colleagues (Nee et al., 1992, 1994; Harvey et al., 1994) to investigate historical properties of a

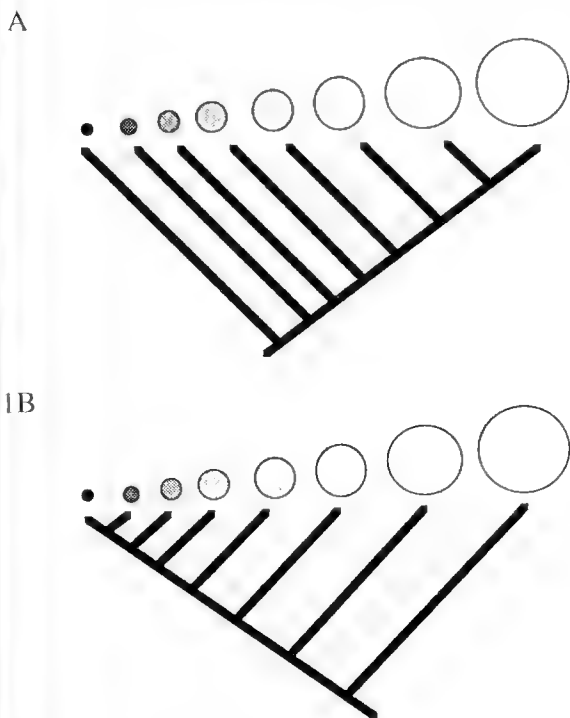


Figure 1. Hypothetical relationships between distribution and phylogeny of a lineage. The size of the circles reflects the geographic area occupied. Different patterns of shading indicate differentiation between taxa. (1A) The range of species is restricted over time since speciation (relictual contraction). Differentiation between taxa occurs subsequent to colonisation of a new habitat. At the same time, taxa also undergo geographic and ecological range expansion. Consequently, the most primitive taxa are the most restricted, the most widespread being derived. (1B) The range of species is restricted with each speciation event (adaptive contraction). Differentiation between taxa occurs within an area subsequent to colonisation. As taxa adapt to local conditions, they become more restricted in geographic and ecological range. Consequently, the most widespread taxa are the most primitive; most restricted derived.

clade using the geometric distribution of coalescent events in a reconstructed molecular phylogeny. If time is scaled by the expected interval between coalescences ($1/[n(n-1)/2]$, Kingman, 1982), then a linear relationship results between the number of lineages and scaled time (Nee et al., 1995). However, if, instead of being linear, the relationship is

1. convex, then the time between coalescences is greater than expected, consistent with a population/species that was expanding during this period in history;
2. concave, then the time between coalescences is less than expected, consistent with a population/species that was shrinking during this period in history.

This theory is used to examine range expansion/contraction of two lineages during their evolutionary history:

1. the *planitibia* clade of Hawaiian 'picture-winged' *Drosophila* (DeSalle, 1995); and
2. two Kauai clades of Hawaiian silverswords, genus *Dubautia* (Baldwin and Robichaux, 1995).

Methods

Hawaiian Tetragnatha

Preliminary analysis of phylogenetic relationships have been conducted for two clades of Hawaiian *Tetragnatha* that differ in vagility: The actively foraging spiny leg clade and the more sedentary web-building 'elongate' clade (Gillespie and Croom, 1995). Analysis of the 'spiny-leg' clade was conducted using fixed differences between allozyme loci for 5–30 individuals from 1–5 populations of the species in the 'spiny leg' clade. The allozymes GPDH, G3PDH, 6PGDH, IDH-1, IDH-2, ME, PGI and PGM were used (Richardson et al., 1986). For the 'elongate' clade phylogenetic relationships among species were examined using morphological information only (30 characters related to cheliceral armature, leg spination, color of the cephalothorax and abdomen and structure of the male palp) (Gillespie and Croom, 1995). Characters were analyzed using parsimony in PAUP (Swofford, 1993), and were scaled for equal character weighting regardless of the number of states.

Hawaiian 'picture-winged' *Drosophila*:

D. planitibia clade

Phylogenetic relationships have been established for the *planitibia* clade of Hawaiian 'picture-winged' *Drosophila* using mtDNA RFLPs (DeSalle, 1995). The *planitibia* clade comprises

the following taxa: *D. cyrtoloma* Hardy and Kaneshiro, *D. melanocephala* Hardy, *D. hanau-lae* Hardy, *D. neoperkinsi* Hardy and Kaneshiro, *D. obscuripes* Grimshaw, *D. nigribasis* Hardy, *D. oahuensis* Grimshaw and *D. neopicta* Hardy and Kaneshiro (alpha clade), and *D. silvestris* Perkins, *D. heteroneura* Perkins, *D. planitibia* Hardy, *D. differens* Hardy and Kaneshiro, *D. hemipeza* Hardy, and *D. neopicta* Hardy and Kaneshiro (beta clade). The distance between species was examined using a Kitch analysis (Phylip, Felsenstein, 1993), which is based on the assumption of constant evolutionary rates.

Hawaiian silverswords

Phylogenetic relationships have been established for the Hawaiian silverswords using ITS region sequences (Baldwin and Robichaux, 1995). For this study, two clades with representatives confined to Kauai (except where noted) were used: *D. latifolia* (A. Gray) Keck, *D. paleata* A. Gray, and *D. raillardoides* Hillebr. (one clade), and *D. imbricata* H. St. John and G. Carr, *D. knudsenii* Hillebr., *D. laevigata* A. Gray, *D. laxa* Hook and Arnott (Kauai, Oahu, Maui), *D. pauciflorula* H. St. John and G. Carr, *D. microcephala* Skottsb., *D. plantaginea* Gaud. (Kauai, Oahu, Maui, Hawaii) (second clade). As with the *Drosophila*, The distance between species was examined using a Kitch analysis.

Results

Hawaiian *Tetragnatha*

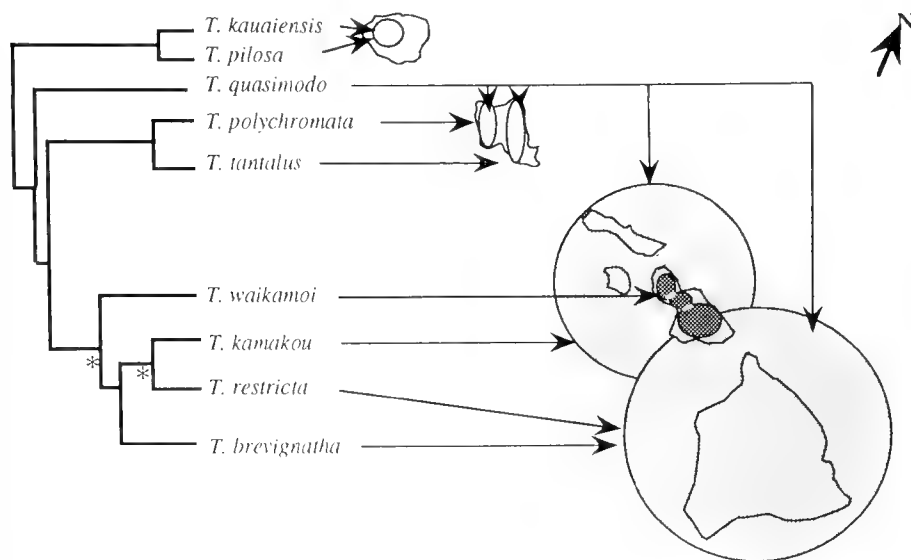
The 'spiny-leg' clade allozyme results yielded large genetic distances between species (considering polymorphic loci only, Nei's $D > 1$ between *T. pilosa* and both *T. brevignatha* and *T. restricta*). The pattern of relationships is shown in Figure 2A. The morphological characters for the 'elongate' clade gave two equally parsimonious trees, length 61 (CI 0.731, RI 0.775) (Fig. 2B shows strict consensus) (Gillespie and Croom, 1995).

Hawaiian 'picture-winged' *Drosophila*:

D. planitibia clade

Distances between nodes were transformed by multiplying inter-node intervals by $n(n-1)/2$ (Nee et al., 1995). The number of lineages were then plotted against the transformed distances. The result was a convex curve, indicating a decreasing rate of branching as the present time is approached (Fig. 3A). This suggests that population sizes have been expanding over the phylogenetic history of this clade.

2A



2B

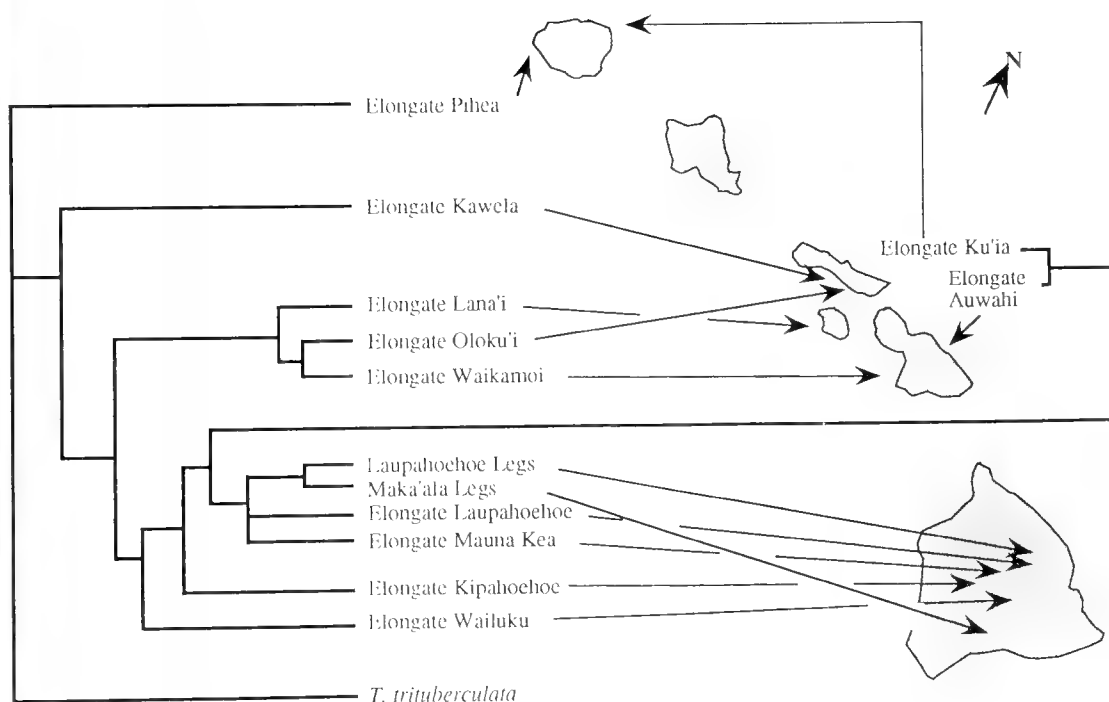


Figure 2A. Pattern of distributional change of the Hawaiian 'spiny leg' *Tetragnatha* through the Hawaiian archipelago based on allozyme data. 2B. Phylogeny of the 'elongate' clade of Hawaiian *Tetragnatha* based on morphological characters (from Gillespie and Croom, 1995). Because representatives of the 'elongate' clade have not yet received formal descriptors, a taxonomic unit was defined for the purpose of the analysis as a population exhibiting a distinct set of characters unique to a given island.

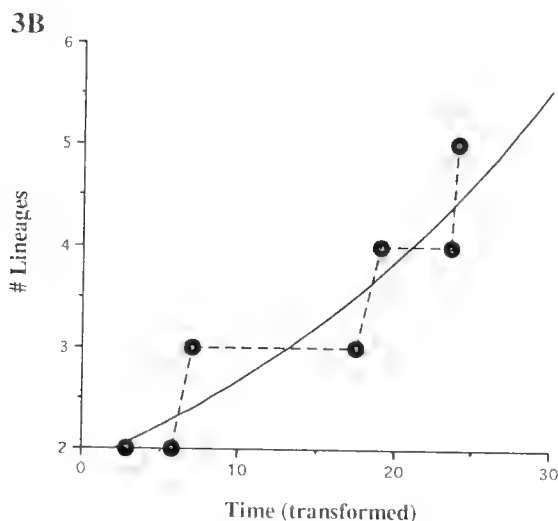
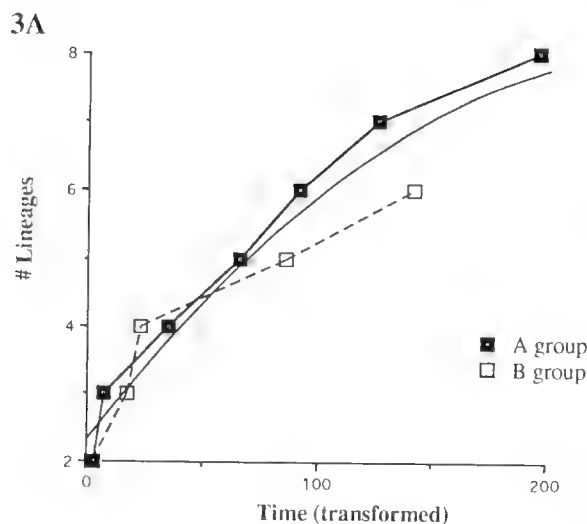


Figure 3A. *Drosophila: Planitibia* Lineage. The curve for the alpha group was not significant (uniform conditional test, Cox and Lewis, 1966: Kolmogorov test statistic, $D = 0.248$, $n = 7$, $0.10 < p < 0.15$), and can only be considered a tendency. However, the curve for the beta group was significant ($D = 0.438$, $n = 6$, $p < 0.01$). 3B. *Dubautia*: Two Lineages from Kauai. The uniform conditional test showed that the curve was significant (Kolmogorov test statistic, $D = 0.275$, $n = 9$, $p < 0.05$).

Hawaiian silverswords

As for the *Drosophila*, the number of lineages were plotted against transformed distances. The result was a concave curve, indicating an increasing rate of branching as the present time is approached (Fig. 3B). This suggests that

population sizes have been decreasing over the phylogenetic history of this clade.

Discussion

Natural factors affecting distributional range

For the 'spiny-leg' (vagile) species of Hawaiian *Tetragnatha*, the allozyme results showed that:

1. Taxa on any one island tend to be most closely related to taxa on other islands;
2. In general, the most derived taxa occur on the youngest island and have the broadest ecological and geographical range.

It might be argued that this effect is an artifact of the larger size of the youngest island. However, all species on the youngest island (Hawaii) range from 300 to >2000 my, and occur in dry — wet forest on all five volcanoes as well as on Maui, whereas on the older islands (Oahu and Kauai) single species are confined to narrow elevational and environmental ranges and are endemic to single volcanoes within each island. In *T. quasimodo*, a relatively ancestral species that is found throughout the islands, populations on the youngest islands have a much greater geographic and ecological range than those on the older islands, consistent with all the other species in the clade. The phylogeny of the 'elongate' clade of Hawaiian *Tetragnatha* suggests that:

1. certain groups have diversified within an island (cf Hawaii Island);
2. The most derived taxa occur on the youngest island; and
3. ranges are smaller for groups that have diversified within an island.

The molecular phylogenies of the Hawaiian *Drosophila* and silverswords revealed intriguing results, and showed the usefulness of this type of analysis for examining changes in distribution through the evolutionary history of a lineage. The *Drosophila* showed a pattern of increasing population size in the component species through the phylogeny of the lineage. This pattern is consistent with the model presented above: *Drosophila* tend to speciate between land masses only, likely because of substantial gene flow prohibiting species formation within islands. As a consequence, speciation will be associated with colonisation of a new land mass, and rapid expansion of the newly derived species, as indicated in Figure 3A. Similarly, for the Kauai silverswords, the large number of species with closest relatives on the same island suggests that local differentiation is possible. As a consequence, speciation

is associated with decreasing population sizes of the derived species as indicated in Fig. 3B.

Anthropogenic factors affecting distributional range

Many species are likely to be products of natural restriction, maintaining healthy and abundant populations within these limited ranges. However, many species are restricted as a direct consequence of anthropogenic restriction on an otherwise widespread population. Two examples from Hawaii are considered.

Tetragnatha albida Gillespie occurs in remnant dry forest of Auwahi, East Maui, a discrete dryland community on unweathered lava with little soil formation (Gillespie, 1994). Individuals build webs in the trees at night, and spend the day camouflaged against white lichen that covers many of the trees. Auwahi is recognised as the finest dryland forest in the Hawaiian Islands (Rock, 1913). However, despite its high diversity of dry forest tree species, many of these trees are not reproducing (Medeiros et al., 1986). More importantly for the unique spider fauna, the aggressive ant *Pheidole megacephala* (Fabricius) is found immediately below the range of *T. albida*, and appears to be expanding its range upwards (Medeiros, pers. comm.). Ants are the most notorious of all alien invertebrate predators because of their effect on the native Hawaiian biota (Perkins, 1913; Howarth, 1985; Howarth and Medeiros, 1989; Gillespie and Reimer, 1993), and are likely responsible for the extirpation of *T. albida* from much of its native range: *T. albida* is part of a phylogenetically derived lineage of Hawaiian *Tetragnatha*, and most likely its historical range was broad. The population would probably respond well to active management of alien species.

A second species of tetragnathid, *Doryonychus raptor* Simon, is almost entirely confined to small, remnant pockets of lowland forests directly below high waterfalls on the island of Kauai. *D. raptor* exhibits one of the most remarkable morphological features ever found in spiders (Simon, 1900; Gillespie, 1992b): The prolateral claws on the tarsi of leg pairs I and II of *D. raptor* are immensely elongated and the spider captures insects using only these claws to impale prey and draw them to the chelicerae in a single, rapid movement. The spider is phylogenetically ancient (Gillespie et al., 1994), and its small distributional range may reflect its evolutionary 'relictual' nature. However, within its small range, the species is abundant. Never-

theless, because many aggressive ants are broadly expanding their ranges in lowland habitats throughout the Hawaiian Islands, species such as *D. raptor* are extremely vulnerable to extirpation.

In conclusion, the identification of species with naturally restricted ranges can allow the adoption of suitable management practices for mitigating the impact of anthropogenic disturbance. Novel ecological interactions, such as competition and predation by alien species, are likely to affect extinction much more rapidly than changes that occur over evolutionary time. The form of a management plan, and the ability of a species to respond, will be affected by its natural distributional range, and, as is argued here, it is also likely to be a product of its phylogenetic legacy.

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References

- Baldwin, B.G. and R.H. Robichaux., 1995. Historical biogeography and ecology of the Hawaiian silver-sword alliance (Asteraceae): New molecular phylogenetic perspectives. Pp. 259–287 in: Wagner W.L. and Funk, V.A (eds), *Hawaiian biogeography: evolution on a hot spot archipelago*. Smithsonian Institution Press: Washington.
- Ball, G.E., 1985. Reconstructed phylogeny and geographical history of genera of the tribe Galeritini (Coleoptera: Carabidae). Pp. 276–321 in: Ball, G.E. (ed.), *Taxonomy, phylogeny and zoogeography of beetles and ants*. Dr. W. Junk: Dordrecht.
- Bush, G.L. and Howard., D.J., 1986. Allopatric and non-allopatric speciation: assumptions and evidence. Pp. 411–438 in: Karlin, S. and Nevo, E. (eds) *Evolutionary processes and theory*. Academic Press: New York.
- Carson, H.L., 1968. The population flush and its genetic consequences. Pp. 123–137 in Lewontin, R.C. (ed.), *Population biology and evolution*. Syracuse University Press: Syracuse, New York.

- Carson, H.L., 1982. Speciation as a major reorganization of polygenic balances. Pp. 411–433 in: Barigozzi, C. (ed.), *Mechanisms of speciation*. Liss: New York.
- Carson, H.L. and Kaneshiro, K.Y., 1976. *Drosophila* of Hawaii: systematics and ecological genetics. *Annual Review of Ecology and Systematics* 7: 311–346.
- Carson, H.L. and Templeton, A.R., 1984. Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annual Review of Ecology and Systematics* 15: 97–131.
- Cesaroni, D., Allegrucci, G., Caccone, A., Cobolli Sbordoni, M., De Mattheis, E., Di Rao, M. and Sbordoni, V., 1981. Genetic variability and divergence between populations and species of *Nesticus* cave spiders. *Genetica* 56: 81–92.
- Cox, D.R. and Lewis, P.A.A., 1966. *The statistical analysis of series events*. Methuen: London.
- Cox, G.W., and Ricklefs, R.E., 1977. Species diversity, ecological release, and community structuring in Caribbean land bird faunas. *Oikos* 29: 60–66.
- Croom, H.B., Gillespie, R.G. and Palumbi, S.R., 1991. Mitochondrial DNA sequences coding for a portion of the RNA of the small ribosomal subunits of *Tetragnatha mandibulata* and *Tetragnatha hawaiiensis* (Araneae, Tetragnathidae). *Journal of Arachnology* 19: 210–214.
- Darlington, P.J., Jr., 1957. *Zoogeography: The geographical distribution of animals*. John Wiley and Sons, Inc.: New York. xi + 675 pp.
- Darlington, P.J., Jr., 1959. Area, climate and evolution. *Evolution* 13: 488–510.
- Darlington, P.J., Jr., 1971. The carabid beetles of New Guinea. Part IV. General considerations; analysis and history of fauna; taxonomic supplement. *Bulletin of the Museum of Comparative Zoology* 142: 130–337.
- DeSalle, R., 1995. Molecular approaches to biogeographic analysis of Hawaiian Drosophilidae. Pp. 72–89 in: Wagner, W.L. and Funk, V.A. (eds), *Hawaiian biogeography: evolution on a hot spot archipelago*. Smithsonian Institution Press: Washington.
- Erwin, T.L., 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. Pp. 539–592 in: Erwin, T.L., Ball, G.E., Whitehead D.R. and Halpern, A.L. (eds), *Carabid beetles: their evolution, natural history and classification*. Dr. W. Junk: The Hague.
- Erwin, T.L., 1985. The taxon pulse: A general pattern of lineage radiation and extinction among carabid beetles. Pp. 437–472 in Ball, G.E. (ed.), *Taxonomy, phylogeny and zoogeography of beetles and ants*. Dr. W. Junk: Dordrecht.
- Felsenstein, J., 1993. PHYLIP (Phylogeny Inference Package) Version 3.5c. Distributed by author at Department of Genetics, University of Washington, Seattle, WA 98195, USA.
- Gillespie, R.G., 1991a. Hawaiian spiders of the genus *Tetragnatha*: I. Spiny Leg Clade. *Journal of Arachnology* 19: 174–209.
- Gillespie, R.G., 1991b. Predation through impalement of prey: The foraging behavior of *Doryonychus raptor* (Araneae, Tetragnathidae). *Psyche* 98: 337–350.
- Gillespie, R.G., 1992a. Hawaiian spiders of the genus *Tetragnatha* II. Species from natural areas of windward East Maui. *Journal of Arachnology* 20: 1–17.
- Gillespie, R.G., 1992b. Impaled prey. *Nature* 355: 212–213.
- Gillespie, R.G., 1993. Biogeographic pattern of phylogeny among a clade of endemic Hawaiian spiders (Araneae, Tetragnathidae). *Memoirs of the Queensland Museum*. 33: 519–526.
- Gillespie, R.G., 1994. Hawaiian spiders of the genus *Tetragnatha*: III. *T. acuta* clade. *Journal of Arachnology* 22: 161–168.
- Gillespie, R.G. and Croom, H.B., 1995. Comparison of speciation mechanisms in web-building and non-web-building groups within a lineage of spiders. Pp. 121–146 in: Wagner, W.L. and Funk, V.A. (eds), *Hawaiian biogeography: evolution on a hot spot archipelago*. Smithsonian Institution Press: Washington.
- Gillespie, R.G. and Reimer, N., 1993. The effect of alien predatory ants (Hymenoptera, Formicidae) on hawaiian endemic spiders (Araneae, Tetragnathidae). *Pacific Science* 47: 21–33.
- Gillespie, R.G., Croom, H.B. and Palumbi, S.R., 1994. Multiple origins of a spider radiation in Hawaii. *Proceedings of the National Academy of Sciences USA* 91: 2290–2294.
- Harvey, P.H. and Pagel, M.D., 1991. *The comparative method in evolutionary biology*. Oxford Series in Ecology and Evolution. Oxford Univ. Press, Oxford.
- Harvey, P.H., May, R.M. and Nee, S., 1994. Phylogenies without fossils. *Evolution* 48: 523–529.
- Howarth, F.G., 1985. Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. Pp. 149–179 in: Stone, C.P. and Scott, J.M. (eds), *Hawaii's terrestrial ecosystems: preservation and management*. University of Hawaii Press: Honolulu.
- Howarth, F.G. and Medeiros, A.C., 1989. Non-native invertebrates. Pp. 82–87 in: *Conservation biology in Hawaii*. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu.
- Howden, H.F., 1985. Expansion and contraction cycles, endemism and area: the taxon cycle brought full circle. Pp. 473–487 in: Ball, G.E. (ed.), *Taxonomy, phylogeny and zoogeography of beetles and ants*. Dr. W. Junk: Dordrecht.
- Johnston, D.W., 1975. Ecological analysis of the Cayman Island avifauna. *Bulletin of the Florida State Museum of Biological Sciences* 19: 235–300.

- Jones, M.J., Lace, L.A., Hounscome, M.V. and Hamer, K., 1987. The butterflies and birds of Madeira and La Gomera: taxon cycles and human influence. *Biological Journal of the Linnean Society* 31: 95–111.
- Kingman, J.F.C., 1982. The coalescent. *Stochastic Processes and Applications* 13: 235–248.
- Larson, A., Wake, D.B., Maxson, L.R. and Highton, R., 1981. A molecular phylogenetic perspective on the origins of morphological novelties in the salamanders of the tribe Plethodontini (Amphibia, Plethodontidae). *Evolution* 35: 405–422.
- Liebherr, J.K. and Hajek, A.E., 1990. A cladistic test of the taxon cycle and taxon pulse hypotheses. *Cladistics* 6: 39–59.
- MacArthur, R.H., Diamond, J.M. and Karr, J.R., 1972. Density compensation in island faunas. *Ecology* 53: 330–342.
- Maddison, W.P. and Maddison, D.R., 1992. *MacClade, version 3, analysis of phylogeny and character evolution*. Sinauer Assoc., Sunderland, Mass.
- Medeiros, A.C., Loope, L.L. and Cole, F.R., 1986. Distribution of ants and their effects on endemic biota of Haleakala and Hawaii Volcanoes National Parks: a preliminary assessment. Pp. 39–52 in *Proceedings of the 6th Conference of Natural Science: Hawaii*.
- Mindell, D.P., Sites, J.W. and Graur, D., 1989. Speciation evolution: a phylogenetic test with allozymes in *Sceloporus*. *Cladistics* 5: 49–61.
- Moran, N.A., 1988. The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. *American Naturalist* 132: 681–706.
- Nee, S., Mooers, A. and Harvey, P.H., 1992. The tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences USA* 89: 8322–8326.
- Nee, S., May, R.M. and Harvey, P.H., 1994. The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society, London* 344: 305–311.
- Nee, S., Holmes, E.C. and Harvey, P.H., 1995. Inferring population history from molecular phylogenies. *Philosophical Transactions of the Royal Society, London* 349: 25–32.
- Otto, C., and Svensson, B.S., 1982. Structure of communities of ground-living spiders along altitudinal gradients. *Holarctic Ecology* 5: 35–47.
- Perkins, R.C.L., 1913. Introduction (to Fauna Hawaiiensis). Vol. I. Pp. xv–ccxxviii in: D. Sharp (ed.), *Fauna Hawaiiensis*. Cambridge University Press: Cambridge.
- Pregill, G.K. and Olson, S.L., 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annual Review of Ecology and Systematics* 12: 75–98.
- Reimer, N.J., Beardsley, J.W. and Jahn, G., 1990. Pests in the Hawaiian islands. Pp. 40–50. in: Vander Meer, R.K., Jaffe, K. and Cedenio, A. (eds), *Applied myrmecology: a world perspective*. Westview Press: Boulder, Colorado.
- Richardson, B.J., Baverstock, P.R. and Adams, M., 1986. *Allozyme electrophoresis. A handbook for animal systematics and population studies*. Academic Press: New York.
- Ricklefs, R.E., 1990. *Ecology, 3rd edn. Regulation of community structure*. W.H. Freeman and Company, New York. [Pp. 748–775].
- Ricklefs, R.E. and Cox, G.W., 1972. Taxon cycles in the West Indian avifauna. *American Naturalist* 106: 195–219.
- Ricklefs, R.E. and Cox, G.W., 1978. Stage of taxon cycles, habitat distribution and population density in the avifauna of the West Indies. *American Naturalist* 112: 875–895.
- Rock, J.F., 1913. The indigenous trees of the Hawaiian Islands. Published privately, Honolulu. Reprinted with introduction by Sherwin Carlquist and addendum by D. R. Herbst, 1974. Charles E. Tuttle Co.: Rutland, Vermont, USA.
- Rosenzweig, M.L., 1978. Competitive speciation. *Biological Journal of the Linnean Society* 10: 275–289.
- Rosenzweig, M.L., 1990. Ecological uniqueness and loss of species: commentary. Pp. 188–198 in: Orians, G.H., Brown, G.M. Jr., Kunin, W.E. and Swierzbinski, J.E. (eds), *The preservation and valuation of biological resources*. University of Washington Press: Seattle.
- Simon, E., 1900. *Arachnida: Fauna Hawaiiensis* 2(5): 443–519, pls 15–19.
- Slatkin, M., 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16: 393–430.
- Slatkin, M., 1987. Gene flow and the geographic structure of natural populations. *Science* 236: 787–792.
- Swofford, D.L., 1993. *PAUP. Phylogenetic analysis using parsimony, version 3.1.1*. Smithsonian Institution, Washington, DC.
- Wilson, E.O., 1959. Adaptive shift and dispersal in a tropical ant fauna. *Evolution* 13: 122–144.
- Wilson, E.O., 1961. The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* 95: 169–193.
- Wood, T.K., 1980. Divergence in the *Enchenopa binotata* Say complex (Homoptera: Membracidae) effected by host plant adaptation. *Evolution* 34: 147–160.
- Wood, T.K. and M.C. Keese., 1990. Host-plant-induced assortative mating in *Enchenopa* tree-hoppers. *Evolution* 44: 619–628.
- Wright S., 1951. The genetical structure of populations. *Annals of Eugenics* 15: 323–354.

POPULATION BIOLOGY OF SOCIAL INSECT CONSERVATION

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Abstract

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Social insects, especially ants and termites, are keystone species in most non-arctic terrestrial ecosystems, but their special features have received little attention in conservation discussions. Both plants and other animals are affected by social insects as keystone species. Despite the abundance of species it may be that rather few in any one location are critical to understanding the ecosystem, because of the mosaic nature of the distributions of the dominant species. Social insects present a wide array of life patterns within the broad sway of sociality, varying in having colonies which are annual or perennial, multi- or single-nested, and multi- or single-queened. Populations of social insects may often be much more vulnerable than they appear on the basis of numbers of individuals: the reproductive division of labor means that the effective population size may be small for a species of apparently reasonable abundance. Factors increasing effective population size occur in many species, especially rare ones, but it is uncertain these represent adaptations to rareness. In eusocial Hymenoptera, many species, probably most, show inbreeding depression of a special kind due to the production of sterile males caused by homozygosity at the sex locus. In many termites, on the other hand, colonies pass naturally through cycles of inbreeding and outbreeding. Socially parasitic ants which habitually inbreed appear to have evolved a different means of sex-determination and do not show inbreeding depression. Differences in the mode of colony formation between species also lead to difference in the longevity of colonies, dispersal abilities, and the robustness of populations to disturbance. The greatest threats to social insects, apart from humans, are other social insects, and this applies also to invading ant pest species, which tend to have particularly strong impacts on native species. Social insects thus form a vital part of ecosystems, but also impel the need to accept long-term studies because of the slow pace at which their populations change.

Introduction

Invertebrates generally differ from vertebrates in the conservation problems they are prone to because of the scale on which they live. Even a small area can contain a large population, so that considerations such as the area of habitat required and problems of a small population size (leading, at least potentially, to inbreeding depression) can be less important and more easily solved. For such populations, habitat loss can remove whole populations without an intervening stage of fragility.

Social insects, however, differ in several important aspects from other invertebrates. We can recognize three major features that characterize social insects and are important in their population biology and in the population biological aspects of their conservation. First, the ratio of population size to biomass is small. Only a small number of individuals reproduce and the effective population size maintained in a given

area can be small and comparable to that of many vertebrates. Yet, the non-reproductive workers constitute a large biomass which affects both the food requirements of the population and the impact of the population on its environment. Second, the life of social insects normally centres around a nest, which makes them sedentary and can restrict dispersal. In that respect their population biology can resemble that of plants rather than of other insects. Third, most social insects (ants, bees and wasps) belong to the order Hymenoptera and have a male-haploid sex-determination system. This genetic mechanism affects some genetic population characteristics, particularly the effective population size and the genetic load resulting from the sex-determination mechanism.

Our aim here is to describe how these features, which are characteristic of social insects, affect their populations and in which ways they can influence their conservation.

The role of social insects in ecosystems

One criterion that can be used when setting priorities for conservation is to what extent other species depend on the species in question (Soulé, 1987). Without focusing on any single species, we can state that social insects in general form an important group both in ecosystems in general and in having important mutual relationships with other organisms, plants as well as animals.

The social life pattern has made social insects evolutionarily very successful, not so much in species diversity but in biomass. Social Hymenoptera make only about 10% of all described hymenopteran species, but the estimates from South-American tropical rainforests show that social insects make more than a quarter of all animal biomass, and c. 80% of all insect biomass (reviewed by Wilson, 1990). It is reasonable to assume that they have a key role in the energy budgets of many other ecosystems, although the ant biomass in temperate grassland areas is only 1–15% of all invertebrates (Pisarski, 1978). The diversities of social insect species are highest in the tropics, except of bumblebees that exist mainly in temperate areas. Of the major groups of social insects, termites and stingless bees occur mainly in tropics and subtropics. The major centres of social wasps are partly in south-east Asia (vespine wasps) and in neotropics (polybine wasps).

Interspecific competition among ants has led to dominance hierarchies between species, and the dominant species can largely influence the composition of the whole ant community. This has led to so called ant mosaics (Leston, 1978; Majer, 1993), found particularly in tropical forests. Replacement of the dominant species can lead to a large change in the assemblage not of only ant species but also of other arthropods (perhaps even vertebrates) as well. In fact, Gilbert (1980) suggested as one of the research priorities for neotropical conservation biology 'autecology of link species, keystone mutualists and dominant ant species'. Majer (1993) notes that ant mosaics become rarer as one moves away from the tropics.

Social insects affect their environment also by building nests and by manipulating the foraging areas. These activities create niches for many other organisms, and indeed, the nests of social insects harbour many different guests — and parasites. Some of the best studied examples come from the *Maculinea* butterflies, the big blues, whose caterpillars live in colonies of the *Myrmica* ants and whose life cycles depend com-

pletely on the host ants. There have been several national extinctions of *Maculinea* species in western Europe (five species live in Europe). The conservation of the butterfly populations requires simultaneous attention on the host ant populations, and active management on these lines has been carried out to reintroduce the large blue (*M. arion*) in Britain (Elmes and Thomas, 1992; Thomas, 1995). Similar situations are expected in Australia, where the lycaenid butterflies include species depending on the care provided by ants (New, 1993).

As regards the plants, the main roles of social insects are in protecting them against herbivores (which has led to the evolution of special domatia, extrafloral nectaries and food bodies by some plants (Beattie, 1985)), in spreading seeds, and as pollinators. For example, Handel et al. (1981) counted that 13 of 45 herbaceous plant species in a mesic forest had seeds dispersed by ants, and they comprised ca 40% of the above-ground herbaceous biomass. Ants contribute significantly to the population dynamics of such myrmecochores and shape the structure of the whole plant community. They are also important for the viability of some rare and endangered plant populations. Although bees are major pollinators of angiosperms, social bees have generally a less important role. They can, however be locally important. Some bees visit only a few closely related species of plants, and the protection of such oligolectic bees relies on the preservation of these plants. At the same time specialist pollinators can be important for the success of the plant populations. Such a close relationship exists between *Aconitum septentrionale* and its pollinator, the bumblebee *Bombus consobrinus*, both of them being rare and endangered in northernmost Europe (Pekkarinen, 1979).

The relatively low species diversity of social insects, at least when compared to many other insects, makes it feasible to use the phylogenetic approach for defining priority areas to protect the worldwide species diversity. Bumblebees of the *Bombus sibiricus*-group comprise one of the first taxonomic groups where this approach has been applied, although the authors note that conservation of bumblebees is not yet generally considered to have a high priority (Williams et al., 1993). There are, however, reports indicating that bees are generally declining (O'Toole, 1993).

Social insect life patterns

Social insect life patterns vary enormously, and their societies can be classified on several bases.

We present here some basic features (Crozier and Pamilo, 1996), all of these adding important aspects also to conservation, mainly because they affect either the effective population size or dispersal.

Annual vs perennial colonies. Bumble bees, many primitively social bees, and many social wasps have annual colonies. They have a solitary phase, with a female (or a group of females) starting a colony and taking care of the first brood, after which the offspring will stay as helping individuals raising additional broods. The colony has first an ergonomic stage when it grows, and the sexual offspring are produced towards the end of the season when the colony moves to a reproductive stage (Oster and Wilson, 1978). Honeybees, stingless bees, swarm-founding wasps, and all ants and termites have perennial colonies. A colony can have a short solitary period if a single female establishes the colony, but after that the colony can survive several years and produce sexuals repeatedly.

Independent vs dependent colony foundation. There are two major modes of nest foundation: independent and dependent. Independently founding females establish new nests without any help from workers, either singly or in small groups. Dependent nest founding relies on workers helping the queen. Dependent nest foundation commonly takes place by budding or fission, in which a new nest is established by workers and queens departing from the parental nest. New nests can also in some ants be established by help of alien species, in form of temporary social parasitism. The queen intrudes into a host colony, and the host workers raise the first brood, after which the colony gradually turns into that of the intruding species.

Monogynous vs. polygynous colonies. Many social insects have a single reproductive female, a queen, in their nests and the colonies are called monogynous. This is the case in the honeybees, most other eusocial bees, many eusocial wasps, the majority of termites and many ants. This is, however, not a rule and about half of the European ant species have polygynous colonies, i.e. they have several to many reproductive females per nest (Buschinger, 1974). Some wood ants of the *Formica rufa* group have up to hundreds of queens in their mounds (Rosengren and Pamilo, 1983). Even if a colony has many queens, they may not share reproduction evenly and their contributions have a non-zero variance, i.e. there exists a reproductive skew (Keller and Reeve, 1994; Pamilo and Crozier, 1996).

Monodomous vs. polydomous colonies. A single nest usually forms a colony and defends its

nest and/or foraging area against competing colonies. Such single-nest colonies are termed monodomous. It is, however, common particularly in some ants that neighbouring nests are connected to each other and exchange individuals, brood and food. Such multinest colonies are termed polydomous. It is evident that such polydomous colonies can effectively occupy and dominate a habitat patch. In an extreme form, when the network of interconnected nests covers a large area, it has been called a supercolony, and if there is no hostility within the whole population, the population is termed unicolonial. Unicolonial species appear to become pests more often than other species, but this apparent trend may simply indicate that many unicolonial species remain to be detected.

Effective population size

Vulnerability of populations can be caused by deterministic or stochastic factors. Stochastic factors depend on the population size and its fluctuations, and on the environmental stochasticity. As mentioned above, the ratio of effective population size to biomass is generally low, or very low, in social insects. The territory of a single ant nest can cover several hectares, yet there may be just one reproductive female in the nest. The density of social insect populations can therefore be low, even though the worker ants are abundant.

The concept of effective population size (N_e) refers to the genetic effects of a finite population size. There are various concepts of N_e , and the one commonly used is the inbreeding effective size. In diploid populations, this N_e is affected by biased sex ratios as follows

$$N_e = 4N_fN_m/(N_f + N_m)$$

where N_f and N_m refer to the numbers of reproductive females and males, respectively. In male-haploid insects, e.g., in ants, bees and wasps,

$$N_e = 9N_fN_m/(2N_f + 4N_m)$$

which for the same numbers of females and males (N_f and N_m) yields smaller effective sizes than in a diploid population, unless the sex ratio is very female-biased. The sex ratios refer to those among breeding individuals, and the effective population size therefore depends on the numbers of matings of males and females. Both sexes are known to mate multiply in many species, but the number of matings by females is commonly low. Many species typically have once-mating females, and the effective number of matings rarely exceeds 2. Exceptions are the honeybees with up to 30 matings in *Apis cerana*,

social wasps of the genus *Vespula*, and leaf-cutting ants (Crozier and Pamilo, 1996).

Whereas multiple mating by females increases the effective population size, multiple mating by males decreases it, because the effect is that several females in the population would carry sperm of the same male. Multiple mating by males is known in several ants, but its general occurrence and genetic effectiveness are poorly known. Males of many species are known to mate only once, as they either die or lose their genitalia when mating (e.g., honeybee).

A further factor reducing effective population size is worker reproduction in social Hymenoptera. Workers in many species are sterile, but in others they can lay haploid eggs developing into males, sometimes workers are assumed to be the major source of males. Even though worker reproduction increases the number of reproductive individuals, it decreases (slightly) the effective population size, because it does not increase the gene pool but simply adds a further step for stochastic fluctuations and increases the variance of male allele frequencies (Crozier, 1979).

The effective size of a social insect population depends clearly not only on the nest density, but on the number of reproductive individuals in the nests, on the reproductive skew among these individuals, and on the genetic mechanisms. The genetically effective population size depends on the effective levels of polygyny and polyandry, and when the contributions of different queens, or those of the males copulating with the same female, are unequal, the effective number of individuals is lower than the actual number. When an individual i contributes a fraction x_i to a colony's production, the effective number of reproductives in the colony is $1/\sum x_i^2$.

Wilson (1971) noted that polygyny tends to occur commonly in rare ant species, habitat specialists and social parasites. He argued that polygyny increases the survivorship of such colonies and populations and that this may have selected for polygyny in these species. Hölldobler and Wilson (1977) developed the idea that polygyny is particularly selected for in two kinds of ants: those with frequently-fragmenting colonies (tramp species) and habitat specialists where the habitat patches are fragmented. Although the pattern is far from clear, it does suggest that rare species associated to specific habitat types can have locally large effective populations because of polygyny. Crozier (1979) further suggested that unicoloniality is an adap-

tation to rarity, with selection on local aggregations occurring as for colony-level selection.

When estimating population sizes in rare species, it is important to not only count the nests but to estimate the number of reproductive females in them. Genetic studies of an endangered ant *Formica cinerea* in northern Europe gives an example. This is a ground-nesting species living in open sandy habitats. Such habitats are rare in northern Europe and constitute either of areas where the retreat of ice stopped for a longer period at the end of last glaciation, or of coastal sand fields. The species is considered vulnerable in Sweden, and it has very fragmented populations in both Sweden and Finland, with some populations occupying only tens of square metres of suitable habitat. Preliminary genetic studies indicate that in some populations the nests are polygynous, whereas in other populations the nests have a single queen (Lindström et al., 1996). Clearly, the effective size, and perhaps vulnerability, of the populations depend also partly on their social organization.

Patterns of population size fluctuations vary among different taxonomic groups. Bumblebees and most social wasps have annual colonies, and their populations fluctuate as a function of weather conditions. Honeybees, stingless bees, ants and termites have perennial colonies, and consequently their populations are more stable. Ant queens can live 10–20 years (Hölldobler and Wilson, 1990), and an estimate of the mean longevity of queens in the ant *Formica exsecta* in natural conditions was over 20 years (Pamilo, 1991). Evaluating the vulnerability of their colonies and estimating the effective population size require information on the age structure of the population.

Baroni Urbani et al. (1973) give some guide lines for estimating population densities of ants, but very few data exist on the demographic parameters needed for population viability analysis. The mortality of incipient colonies, when resulting from independent founding, is high in all groups of social insects. It can take a long time for successful colonies to reach maturity. In annual colonies, this ergonomic stage takes place during a summer, but perennial colonies can grow several years before they start producing sexuals.

Scherba (1963), and Pamilo (1991) estimated annual death rates of nests in two related species of *Formica* ants to be 5–9%, and Scherba estimated the birth rate to be 5–13%. It is a general observation in many ants that mature colonies

outnumber young colonies and populations look very stable (Wilson, 1971: 445). However, demographic data on the turnover rate of nests may not tell about the turnover rate of reproductive individuals if a nest has more than one queen. Wilson (1971) remarked that colonial organization serves as a homeostatic device in damping fluctuations in the numbers of individual insects. It would be important to know if there is any correlation between the density of nests and the number of reproductive individuals per nest in populations where the number of nests shows temporal variation. Elmes (1987) found in a long time series of an ant *Myrmica sulcinodis* in a heathland habitat regenerating after a fire, that the number of queens in the nests fluctuated synchronously in the population, and the fluctuations seemed to follow a cycle of 4–5 years, which probably coincides with the life-span of the queens.

Three categories of colonies can be extremely stable, and in theory immortal (Wilson, 1971: 444), namely polygynous colonies that recruit new queens, colonies that reproduce by budding or fission (resembling vegetative growth), and monogynous colonies that can raise replacement reproductives in the case the colony queen (or either member of the royal pair in termites) dies. It is an important task for population studies of endangered social insect species to try to estimate the relevant demographic parameters and the social organization of colonies. Such information is needed also for common species, as the data on population dynamics of social insects, particularly those with perennial colonies, are few. Yet, these can be keystone species with a significant influence on other taxa in the ecosystem (LaSalle and Gauld, 1993). Vulnerability of even major ecosystem components can in some cases be reduced to simple population size effects in a few keystone species.

If one wants to estimate population size in order to evaluate genetic aspects, one should estimate the number of effectively reproducing individuals. However, for estimating population viability, it may be sufficient to estimate the birth and death rates of colonies, if one assumes that these variables do not interact with changing queen numbers when the population declines. Most life history models of social insects have focused on the growth of colonies (Oster and Wilson, 1978; Bourke and Franks, 1995), and in consequence the dynamics of the whole population are still poorly understood.

Dispersal and fragmentation of populations

The sedentary life style of social insects affects both the turnover of individuals in local populations and dispersal and differentiation between populations. A clear indication of limited dispersal of females in social insects with polygynous colonies is that the coexisting queens are genetically related to each other (Crozier and Pamilo, 1996), and the females therefore seem to have a tendency to stay in their natal colony after mating.

Dependent nest founding, particularly when based on splitting of existing nests, includes limited dispersal (at least of females) and is expected to lead to genetic differentiation of local populations. A comparison of conspecific populations, or pairs of closely related species with different modes of colony foundation and social organisation, suggest that this indeed is the case. A pattern emerging from such comparisons suggests that populations with colony budding have greater genetic differences among subpopulations than populations with independent founding (Table 1). The observed pattern indicates that occasional immigrating females have been frequently eliminated by local ants.

Table 1. Genetic differentiation of populations with different colony types. Differentiation is measured as F_{ST} , and the colony types are M-M: monogynous and monodomous colonies, and P-P: polygynous and polydomous colonies. The study areas range from 1 to 20 km, except in *F. aquilonia*, where it is 400 km.

Species	FST		Reference
	M-M	P-P	
<i>Formica truncorum</i>	0.04	0.19	Sundström (1993)
<i>Formica aquilonia</i>	—	0.18	Pamilo (unpubl.)
<i>Myrmica ruginodis</i>	0.02	—	Seppä and Pamilo (1995)
<i>Myrmica rubra</i>	—	0.20	Seppä and Pamilo (1995)

It is interesting to note, as remarked by Wilson (1971), that the species which reproduce by budding have traded dispersal capacity for longevity of the existing nests. This pattern of colony foundation also means that a species can be slow in recolonizing and re-establishing areas where it has gone extinct. This, however, does not apply to all species in this category, as some of the quickly spreading pest ants have a highly polygynous and polydomous colonial structure.

It is still unclear to what extent social insect populations are subdivided due to restricted dispersal. Hill-topping behaviour of mating swarms has been described in some species, and genetic differentiation within a homogeneous habitat in a population of *Formica transkauca-sica* strongly suggests that dispersal of sexual individuals is restricted in spite of a lack of physical barriers, even though the size of habitat is only 200×1000 m, distances that could be moved by a flying ant (Pamilo, 1983).

The low ratio of population size to biomass, and the restricted dispersal at least in many (but not all) social insect species, suggest that any analyses of population viability should pay attention to the spatial scale even in apparently continuous populations (Lande, 1987).

Inbreeding depression

One of the on-going debates in conservation biology is whether inbreeding depression and genetic erosion contribute significantly to extinction of populations, or whether ecological factors cause extinction before inbreeding has time to significantly influence demography. Hymenopteran species, because of their male-haploidy, have been both predicted (Crozier, 1985) and shown (e.g., Pamilo et al., 1984) to have lower levels of allozyme variation than other insect orders, and variation is particularly low in social species. It is, however, difficult to think that such a lower level of heterozygosity would largely affect the viability of populations (see also Unruh and Messing, 1993). Another consequence of male-haploidy is that recessive, deleterious mutations are effectively selected against in haploid males, and this can reduce inbreeding depression (but see Crozier, 1985, and Werren, 1993, for some complications).

There is one reason to predict that social hymenopteran species can suffer seriously from inbreeding depression. The sex in the honeybee is determined by a single locus in such a way,

that individuals heterozygous for the locus develop into females (workers or new queens), while other genotypes develop into males. Normal males are haploid (hemizygous), but diploid individuals that are homozygous for a sex allele develop also into males. Diploid males are shown to be sterile or inviable. It has been proposed that the same, or similar, sex-determining mechanism exists in most social hymenopterans (Cook and Crozier, 1995). There is clearly strong frequency-dependent selection maintaining allelic diversity at the sex locus. Decreasing variation increases the proportion of diploid males and causes a genetic load. When a female mates once and the male and the female carry an identical sex allele (matched mating), half of the diploid offspring are males.

In the introduced fire ant, *Solenopsis invicta*, in northern America colonies started by a single female producing diploid males do not survive to maturity (Ross and Fletcher, 1986). Some *Formica* ants produce rather high frequencies of diploid males, and monogynous colonies with matched mating can survive the founding stage and reach maturity (Pamilo et al., 1994). The *Formica* females have dependent nest founding, as they take over established nests of another species (subgenus *Serviformica*). The proportion of nests producing diploid males is particularly high in isolated island populations that have very few colonies.

Diploid males occur in *Formica* nests only at a time of normal sexual production. During other times, only workers are produced and diploid males are apparently eliminated at an early developmental stage, as also happens in the honeybee. This effectively reduces the load caused by diploid males, once the colony has survived the founding stage. As the species have evolved mechanisms to eliminate some of the load caused by diploid males, it is too early to conclude how significantly diploid male production contributes to the vulnerability of small and isolated populations (Table 2).

In many termites colonies enter a cycle of inbreeding, when the primary reproductives die and are replaced. The replacement reproductives originate from the same colony and inbreed in it, and a cycle of inbreeding can continue several generations. Such a naturally high level of inbreeding is effective in eliminating any harmful recessive alleles in the same way as male-haploidy in the Hymenoptera, and it can be predicted that termites are unlikely to suffer severely from inbreeding depression when the population size decreases.

Table 2. Possible genetic effects in sparse and fragmented ant populations as a function of colony type (M-M and P-P as in Table 1).

	M-M	P-P
N_c	small	large
Genetic differentiation	gradual	distinct
Sex alleles	few	affected by bottlenecks when colonizing
Genetic load	Diploid male production can cause a load	Dependent nest foundation diminishes the load

Social parasites

Socially parasitic species are known in bees, wasps and ants, but not in termites. Females of socially parasitic species take over nests of other, commonly closely related species, and let the host species raise the larvae. The parasite populations are naturally smaller than those of the host species, and the parasites are often very species specific.

Social parasitism has according to the so called Emery's Rule evolved between two closely related species, or the parasite has evolved directly from the host. Parasitism in ants is particularly common in leptothoracine ants, and many parasitic species are found in isolated populations in mountain areas (Buschinger, 1989). Many of the social parasites are extremely rare and have a restricted geographical distribution.

Because of low population densities, socially parasitic ants are known to inbreed frequently and the sex-locus system of other ants has been evolutionarily replaced (Buschinger, 1989). It is evident that they have often small and isolated populations, and parasitic ants belong to those of the rarest and most endangered species. Hölldobler and Wilson (1990: 212–213) note that parasitic species have a tendency to be polygynous (as many other rare ants do), which increases their effective population sizes.

Introduced species

Some social insects that have been introduced to new areas, accidentally or on purpose, have led to a need to protect the native fauna.

The introduced ants *Solenopsis invicta* (the imported fire ant), *Linepithema humile* (the Argentine ant), *Pheidole megacephala*, and

Wasmannia auropunctata are spreading in different islands and continents. They are all characterized by highly polygynous and polydomous (or unicolonial) colonial structures, and they replace native ants of similar ecological requirements. Whereas the Argentine ant occupies largely urban and other disturbed habitats (at least in Australia), the other three species have also penetrated native ecosystems.

Honeybee is introduced and maintained by humans, and bumblebees are also cultured and introduced for pollination purposes. These introduced bees, particularly the honeybee, can compete with the native bee fauna and can, at least potentially, have undesirable effects on the local bee diversity (see New (1994) for a discussion on this problem).

One important conservation aspect is to preserve the native faunas, because they play important roles in the native ecosystems.

Conclusions

We have shown that social insects, a major part of many ecosystems, have many differences from other invertebrates in characteristics important for conservation. Low dispersal rates and small effective population sizes (in relation to the biomass) make many species liable to be easily endangered (and associated species threatened). This potential vulnerability is increased for hymenopterans by their male-haploidy and the single-locus sex determination system (Table 2). The long life-span of colonies means that population change is slow, necessitating acceptance of the need for studies to be long-term. There is a significant need for manipulation experiments to ascertain the extent of ecosystem-wide effects of changes in the composition of the social insect community.

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References

- Baroni-Urbani, C., Josens, G. and Peakin, G.J., 1978. Empirical data and demographic parameters. Pp. 5–44 in: Brian, M.V. (ed.), *Production ecology of ants and termites*. Cambridge Univ. Press: Cambridge.
- Beattie, A.J., 1985. *The evolutionary ecology of ant-plant mutualisms*. Cambridge Univ. Press: Cambridge.
- Bourke, A.F.G. and Franks, N.R., 1995. *Social evolution of ants*. Princeton Univ. Press: Princeton, New Jersey.
- Buschinger, A., 1974. Monogynie und Polygynie in Insektensozietäten. Pp. 862–897 in: Schmidt, G.H. (ed.), *Sozialpolymorphismus bei Insekten*. Wiss. Verlagsges.: Stuttgart.
- Buschinger, A., 1989. Evolution, speciation, and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera: Formicidae). *Journal of Evolutionary Biology* 2: 265–283.
- Cook, J.M. and Crozier, R.H., 1995. Sex determination and population biology in the Hymenoptera. *Trends in Ecology and Evolution* 10: 281–286.
- Crozier, R.H. 1979. Genetics of sociality. Pp. 223–286 in: Hermann, H.R. (ed.), *Social insects, Vol. I*. Academic Press: New York.
- Crozier, R.H., 1985. Adaptive consequences of male-haploidy. Pp. 201–222 in: Helle, W. and Sabelis, M.W. (eds), *Spider mites, their biology, natural enemies and control, Vol. 1a*. Elsevier: Amsterdam.
- Crozier, R.H. and Pamilo, P., 1996. *Evolution of social insect colonies, sex allocation and kin selection*. Oxford University Press: Oxford.
- Elmes, G.W., 1987. Temporal variation in colony populations of the ant *Myrmica sulcinodis*. I. Changes in the queen number, worker number and spring production. *Journal of Animal Ecology* 56: 559–571.
- Elmes, G.W. and Thomas, J.A., 1992. Complexity of species conservation in managed habitats: interactions between *Maculinea* butterflies and their ant hosts. *Biodiversity and Conservation* 1: 155–169.
- Gilbert, L.E., 1980. Food web organization and the conservation of neotropical diversity. Pp. 11–33 in: Soulé, M.E. and Wilcox, B.A. (eds), *Conservation biology, an evolutionary-ecological perspective*. Sinauer Ass.
- Handel, S.N., Fisch, S.B. and Schatz, G.E., 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bulletin of the Torrey Botanical Club* 108: 430–437.
- Hölldobler, B. and Wilson, E.O., 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64: 8–15.
- Hölldobler, B. and Wilson, E.O., 1990. *The ants*. Springer Verlag: Berlin.
- Keller, L. and Reeve, H.K., 1994. Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution* 9: 98–102.
- Lande, R., 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* 130: 624–635.
- LaSalle, J. and Gauld, I.D., 1993. Hymenoptera: their diversity, and their impact on the diversity of other organisms. Pp. 1–26 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Leston, D., 1978. A neotropical ant mosaic. *Annals of the Entomological Society of America* 71: 649–653.
- Lindström, K., Berglind, S.-A., Pamilo, P., 1996. Variation of colony types in the ant *Formica cinerea*. *Insectes Sociaux* 43: 329–332.
- Majer, J.D., 1993. Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia — its structure and influence on arthropod diversity. Pp. 115–141 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- New, T.R. (ed.) 1993. *Conservation biology of Lycaenidae (Butterflies)*. IUCN: Gland, Switzerland.
- New, T. R., 1994. *Exotic insects in Australia*. Glenagles Publ.: Glen Osmond, Australia.
- Oster, G.F. and Wilson, E.O., 1978. *Caste and ecology of social insects*. Princeton Univ. Press: Princeton, New Jersey.
- O'Toole, C., 1993. Diversity of native bees and agroecosystems. Pp. 169–196 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Pamilo, P., 1983. Genetic differentiation within subdivided populations of *Formica* ants. *Evolution* 37: 1010–1022.
- Pamilo, P., 1991. Life span of queens in the ant *Formica exsecta*. *Insectes Sociaux*, 38: 111–119.
- Pamilo, P. and Crozier, R.H., 1996. Reproductive skew simplified. *Oikos* 75: 533–535.
- Pamilo, P., Sundström, L., Rosengren, R. and Fortelius, W., 1994. Diploid males and colony-level selection in *Formica* ants. *Ethology, Ecology Evolution* 6: 221–235.
- Pamilo, P., Varvio-Aho, S.-L. and Pekkarinen, A., 1984. Genetic variation in bumblebees (*Bombus psithyrus*) and putative sibling species of *Bombus lucorum*. *Hereditas* 101: 245–251.
- Pekkarinen, A., 1979. Morphometric, colour and enzyme variation in bumblebees (Hymenoptera, Apidae, *Bombus*) in Fennoscandia and Denmark. *Acta Zoologica Fennica* 158: 1–60.

- Pisarski, B., 1978. Comparison of various biomes. pp. 326–371 in: Brian, M.V. (ed.) *Production ecology of ants and termites*. Cambridge Univ. Press: Cambridge, U.K.
- Rosengren, R. and Pamilo, P. 1983. The evolution of polygyny and polydomy in mound-building *Formica* ants. *Acta Entomologica Fennica* 42:65–77.
- Ross, K.G. and Fletcher, D.J.C., 1986. Diploid male production — a significant colony mortality factor in the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 19: 283–291.
- Scherba, G., 1963. Population characteristics among colonies of the ant *Formica opaciventris* Emery (Hymenoptera: Formicidae). *Journal of the New York Entomological Society* 71: 219–232.
- Seppä, P. and Pamilo, P., 1995. Gene flow and population viscosity in *Myrmica* ants. *Heredity* 74: 200–209.
- Soulé, M.E., 1987. Introduction. Pp. 1–10 in: Soulé, M.E. (ed.), *Viable populations for conservation*. Cambridge Univ. Press: Cambridge.
- Sundström, L., 1993. Genetic population structure and sociogenetic organization in *Formica truncorum*. *Behavioral Ecology and Sociobiology* 33: 345–354.
- Thomas, J.A., 1995. The ecology and conservation of *Maculinea arion* and other European species of large blue butterfly. Pp. 180–197 in: Pullin, A.S. (ed.), *Ecology and conservation of butterflies*. Chapman & Hall: London.
- Unruh, T.R. and Messing, R.H., 1993. Intraspecific biodiversity in Hymenoptera: implications for conservation and biological control. Pp. 27–52 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Werren, J. H., 1993. The evolution of inbreeding in haplodiploid organisms. Pp. 42–59 in: Thornhill, N.W. (ed.), *The natural history of inbreeding and outbreeding*. University of Chicago Press: Chicago.
- Williams, P.H., Vane-Wright, R.I. and Humphries, C.J., 1993. Measuring biodiversity for choosing conservation areas. Pp. 309–328 in: LaSalle, J. and Gauld, I.D. (eds), *Hymenoptera and biodiversity*. CAB International: Oxon, U.K.
- Wilson, E.O., 1971. *The insect societies*. Harvard Univ. Press: Mass., USA.
- Wilson, E.O., 1990. *Success and dominance in ecosystems: the case of the social insects*. Ecology Inst.: Oldendorf/Luhe, Germany.

CONSERVATION STATUS, THREATS AND HABITAT REQUIREMENTS OF AUSTRALIAN TERRESTRIAL AND FRESHWATER MOLLUSCA

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Abstract

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World-wide, non-marine molluscs have the largest number of documented extinctions, and of IUCN — listed threatened species, of any major group. Despite this, as with other invertebrate groups, they attract little or no attention from organisations and government departments concerned with conservation.

Major impediments to the conservation of non-marine molluscs in Australia, and elsewhere, include the lack of appropriate legislation, lack of concordance with existing protected areas and little public and political interest. An Action Plan for Australian molluscs is being prepared as part of an Action Plan for non-marine molluscs world-wide being coordinated through the Mollusc Specialist Group of IUCN. The plan will bring otherwise inaccessible data to public attention and its recommendations will have application in the conservation of non-marine invertebrates in general.

Many Australian non-marine molluscs have very small ranges and are therefore vulnerable to a wide range of threatening processes. The Australian non-marine molluscan fauna currently comprises 1020 named species-group taxa, 80.2% of which are endemic to one State or Territory. 255 species-group taxa (25% of the total fauna) are currently listed by IUCN as threatened in Australia.

Introduction

Invertebrates comprise a large proportion of biodiversity but are very rarely considered in reserve selection and other conservation initiatives in Australia (e.g., Yen and Butcher, 1992; Ponder, 1992a; New, 1995). A major impediment in utilizing invertebrates is that many groups are poorly known both taxonomically and biologically and few people have the expertise to accurately identify them. In addition, unlike the situation with vertebrates and higher plants, funding has not generally been made available to place important collections on data bases. Some of the better known groups, including some insect groups (e.g. butterflies), are known to contain rare and threatened species. However many of these taxa, like many threatened vertebrates and higher plants, have considerable distributional ranges. By way of contrast, some invertebrates, including certain groups of insects and spiders show marked regional endemism. This is especially true in land and freshwater molluscs and some aquatic crustacean groups, many of which have very restricted ranges (often less than 2 km² — e.g., Solem, 1988). Areas which have a concentration of narrow range endemics ('hot-spots') should have a high priority for conservation once identified.

Such areas are easily missed in a strictly habitat-based approach to conservation.

Non-marine molluscs are one of the best known groups of non-marine invertebrates (see Smith, 1992, for a reasonably up to date listing of named taxa). Non-marine molluscs, as a group, comprise the largest number of recorded extinctions in the last 300 years [284, listed by IUCN (Groombridge, 1993)] — this being far more than combined world-wide bird and mammal extinctions in the same period. To date, mainland Australia has no absolutely confirmed non-marine mollusc extinctions but this will undoubtedly change, given increasing knowledge about the fauna, the large numbers of narrow range endemics and the rapid rate of habitat destruction that will undoubtedly affect a significant number of Australian non-marine molluscs. However, mollusc conservation continues to have a low profile, even in current discussions on invertebrate conservation. For example, in a recent issue of *Victorian Naturalist* (vol. 112, 1995) devoted to invertebrate conservation, molluscs hardly rated a mention.

An important aspect of IUCN conservation strategy is to produce 'action plans' for particular groups. To date (Nov 1995), there has been only one IUCN Action Plan developed for invertebrates, that being for one small group of

insects, Swallowtail Butterflies. The Mollusc Specialist Group (one of the IUCN specialist groups) is well advanced in its production of an Action Plan for all non-marine molluscs of the world. A draft Australian plan has been developed as part of this exercise and some of the findings are summarized below.

The Australian non-marine molluscan fauna

The non-marine fauna of Australia, Lord Howe and Norfolk Islands was catalogued by Smith (1992) who recognised 190 freshwater and 920 terrestrial species, including 52 introduced taxa. On the Australian mainland (including Tasmania), only 14 (1.4%) of the native land and freshwater taxa occur naturally outside Australia, thus the molluscan fauna has a very high endemism even by Australian standards (98.6% compared with mammals 82%; birds 45%; reptiles 89% and vascular plants 85%). The land and freshwater molluscan fauna of Lord Howe Island (69 terrestrial, 16 freshwater species-group taxa) and Norfolk Islands (68 terrestrial and 1 freshwater) is also almost entirely endemic to each island. Since Smith (1992) an additional 119 species-group taxa have been named (to Jun 1995) (Table 1). Smith (1992) estimated that 30–40% of the non-marine fauna remained to be described, but a more likely estimate is that the total non-marine fauna is around 2000 species.

There are 178 species of Australian (excluding Lord Howe and Norfolk Islands) freshwater molluscs recorded by Smith (1992) and 743 species of terrestrial molluscs. Since then (to late 1995) 119 additional species-group taxa [66 freshwater (representing a 37% increase) and 53 terrestrial (7% increase)] have been described bringing the totals to 244 and 796 respectively

and the overall total of named terrestrial and freshwater taxa 1170. Of these 72.1% of the named freshwater fauna (176 species-group taxa) and 69.3% of the named terrestrial fauna (642 species group taxa) are restricted to a single state or territory. Only 14 (1.5%) of these species also occur outside Australia.

For most groups, the work to date has only been descriptive. There are no substantive reviews of most families, and very few phylogenetic treatments. Only two cladistic analyses of non-marine groups have been published, both involving Hydrobiidae (Ponder and Clark, 1990; Ponder et al., 1993). Very little biological information is available, even for common taxa and few detailed distributions have been published.

Terrestrial molluscan fauna

Of the 23 families recognised in the described Australian terrestrial mollusc fauna, the medium to large-sized Camaenidae is by far the most speciose family, with 408 currently valid, named species-group taxa comprising 51.3% of the named terrestrial land snails. The small-sized Charopidae are next (129 named, valid species-group taxa) with 16.2% of the named native terrestrial fauna. Both of these groups, and some other families, contain a large number of unnamed taxa (e.g. Solem, 1991; Stanisc, 1994). In all, nearly half (48%) of the land molluscs of eastern Australia are unnamed (Stanisc, 1994). Other large families include Pupillidae (41 taxa), Bulimulidae (31 taxa), Punctidae (23 taxa), Pupinidae (19 taxa) and Helicarionidae (60 taxa).

Smith (1992) lists 69 native terrestrial molluscs in 10 families on Lord Howe Island. The most diverse are the Helicarionidae (18 species-group taxa), Charopidae (17 species-group taxa),

Table 1. Species-group taxa of Australian freshwater and terrestrial molluscs listed by Smith (1992) with the number of species-group taxa named since added to the totals in brackets. The number in square brackets is the number of species-group taxa restricted to the state or territory, those in the totals columns being the sum of these numbers.

	NSW	Qld	Vic.	SA	WA	NT	Tas.	Total Aus.
Freshwater	42 [11]	56(58) [24]	37(45) [16]	34 [11]	31 [20]	27 [8]	42(98) [86]	178(244) [176]
Terrestrial	140 [79]	234(236) [172]	50 [20]	72(99) [83]	226(230) [201]	71(94) [52]	44 [35]	743(796) [642]
Total	182 [90]	290(294) [196]	87(95) [36]	106(133) [94]	258(262) [221]	98(121) [60]	86(141) [121]	901(1020) [818]

Diplomatinidae (14 species-group taxa) and Punctidae (11 species, with several undescribed, Climo, 1981). The last comprehensive review of the Lord Howe terrestrial molluscan fauna was by Iredale (1944 — see also Stanisic, 1981).

Freshwater molluscan fauna

Australia does not possess a spectacularly diverse freshwater molluscan fauna, having only 18 species of freshwater mussels (Unionoidea: Hyriidae) and very few large-sized gastropods. Apart from the hyriids, corbiculids (2 species) and small numbers of viviparids (6 species) and thiarids (9 species), most of the rest of the fauna (9 families) are of small size. Amongst these, the hydrobiids stand out as being particularly diverse (117 named species-group taxa), many with very restricted distributions (Ponder, 1994) and many remain undescribed. The next largest family, the Planorbidae, has about 40 species. Most families require major revision and more new taxa are known in Assimineidae, Bithyniidae and Glacidorbidae than are currently described. Although the Sphaeriidae was relatively recently revised (Kuiper, 1983), further work on this group is also needed.

For an oceanic island, Lord Howe Island has an exceptional freshwater molluscan fauna. Apart from one record of an ancylid (Ponder, 1981a), there is a remarkable hydrobiid fauna (Ponder, 1982) comprising 15 named species-group taxa in three genera. *Hemistomia minutissima* and another unnamed species live interstitially in sediments in stream beds.

Threatened taxa

Although 255 threatened Australian taxa are listed in the 1994 Red List (Groombridge, 1993) more will be added as details of their distributions and status become available. Other species belong in groups which require taxonomic revision but by far the largest group of unlisted taxa are species which await description. Many undescribed, narrow range camaenids are known, especially from Western Australia, the Northern Territory and Queensland. Charopids are speciose in eastern Australia and many undescribed species have very limited ranges, especially those on limestone outcrops. At present the following numbers of threatened taxa are listed by IUCN (Groombridge, 1993) for each state and territory (T=terrestrial, FW=freshwater) — NSW (mainland 18T, 1FW; Lord Howe Island 4T, 8FW), Queensland

(26T, 13FW), Victoria (13T, 5FW), South Australia (19T, 9FW), Western Australia (63T, 1FW), Northern Territory (21T), Tasmania (7T, 60FW) and Norfolk Island (2T, 1FW).

The current listing of only 6 terrestrial species from both Lord Howe and Norfolk islands does not reflect the true nature of the situation. For example *Placostylus bivaricosus* from Lord Howe is certainly threatened, being restricted to a few very small colonies which suffer high levels of rat predation. Data is urgently needed on the current distributions and status of terrestrial taxa on both islands.

Extinctions

Many of the recorded extinctions of terrestrial molluscs are those on oceanic islands. There have been some extinctions of large land snails on Lord Howe Island, probably mostly due to rats (Smithers et al., 1977) and, possibly, pigs, rather than habitat destruction. A large species, *Epiglypta howinsulae* (Cox), is almost certainly extinct, as is a 'form' (or 'subspecies') of *Placostylus bivaricosus* (Gaskoin), *P. bivaricosus etheridgei* (Hedley), both of which occurred on the well forested southern part of the island. Habitat destruction caused by introduced animals was probably responsible for the extinction of another 'form' of *Placostylus*, *P. cuniculinsulae*, from Rabbit Island (Smithers et al., 1977; Hutton, 1986), as well as other supposed endemic land snails from that island (see Iredale, 1944).

On Norfolk Island, the only recorded freshwater mollusc, the hydrobiid *Posticobia norfolkensis* (Sykes), is now presumed to be extinct (Ponder, 1981b). The environmental degradation of this island and the introduction of feral animals which has resulted in the extinction of several birds and plants has probably affected the terrestrial land snail fauna. Iredale (1945) records the extinction of the land snails of the nearby Phillip Island (3 species) which was completely stripped of vegetation by feral animals by the 1940s and at least 4 species of land snails are now presumed extinct on Norfolk Island itself (R.V.J. Varman, *in litt.*).

There are no published records of confirmed extinctions of non-marine molluscs on the Australian mainland to date. However, this is probably in part because there was a general lack of systematic and/or well documented early collecting of many of the areas now entirely rural and urban. It is probably also a reflection of the poor state of the taxonomy of many of the

groups, particularly the lack of modern comprehensive reviews and revisions resulting in poor information on the current status of many species.

Given the considerable localization and high vulnerability in permanent, mainly lowland streams, many hydrobiids have undoubtedly become extinct in the last 200+ years in areas where this family is known to be diverse (e.g. north coast of Tasmania). The detailed work of Ponder et al. (1993) enables the reporting of at least four suspected extinctions of Tasmanian hydrobiids. *Beddomeia tumida* from Great Lake has not been found since the flooding of that lake in the 1920s. An unnamed species of *Beddomeia* with a distinctive shell morphology from 'Table Cape' collected prior to 1900 was not located in a search of virtually all the streams in this heavily impacted area in 1989. An undescribed species of *Phrantela* was collected from the Serpentine River, SW Tasmania prior to the flooding of this area as part of the new Lake Pedder in 1972. This species has not been found in any of the extant streams and rivers in the area. A population attributed to *Beddomeia lodderae* by Petterd (1889) from Deep Creek, Duck River, but which probably represents a distinct species, cannot now be located (Ponder et al., 1993: 603), this area having been cleared for agriculture.

Drawdown from extraction of artesian water since the turn of the century has resulted in the extinction of many of the artesian (mound) springs associated with the Great Artesian Basin (Habermehl, 1982; Ponder, 1986). Given that the considerable endemic aquatic invertebrate faunas associated with these springs (Ponder, 1986) were not recorded until the 1980s, there have probably also been extinctions of significant undocumented faunas.

Near extinctions of viviparids have been reported in the Murray River, with the only surviving population of one species living in a few irrigation pipelines (Sheldon and Walker, 1993a,b). Another species, extinct in the Murray, is known from a few additional populations. At the time of writing the viviparid in the pipelines are in imminent danger of being exterminated because they pose a nuisance through clogging the spray nozzles (K. Walker, pers. comm.).

About two thirds of Australia's rainforests have been cleared in the last 200 years but the first detailed survey for molluscs in east coast rainforests was undertaken in 1975 in mid-east Queensland. Of the 92 species collected in only

10 sites, 42% were undescribed (Colman and Burch, 1977).

Limestone areas in particular, because of their often highly localised cave and surface faunas, are particularly vulnerable. In the main, these habitats have only begun to be systematically collected in the last 10 years by J. Stanisc. Clearing of trees from limestone areas for rural activities has probably had a serious impact in some areas, as have mining activities.

Forty-five introduced taxa (Smith, 1992) make up 5.1% of the Australian mainland fauna. There are 13 families of terrestrial molluscs and one freshwater family introduced to Australia, the majority of these taxa being found in rural and urban areas, mainly in the southern, south-eastern and south-western coastal areas and Tasmania (Smith, 1981, 1992; Kershaw, 1991). Some helicids (see Smith and Kershaw, 1981; Baker, 1989) and limacid slugs (see Altena and Smith, 1975) are economic pests. Nothing is known about the interactions between native and introduced taxa.

Habitat conservation

The belief that habitats conserved for other organisms (namely vertebrates and higher plants), or on a representative ecosystem basis, will provide effective conservation for invertebrates is well entrenched. Whereas this may be effective for many widely distributed species (which are typically at low risk) it is generally inappropriate for many of the taxa of high conservation significance such as narrow range endemics, including many relict taxa. However, there are some areas where general conservation interests and those of molluscan conservation coincide, either because of general concerns for important habitats such as rainforests, or because of happy accidents, where areas set aside for conservation include areas that are important for narrow range endemic invertebrate taxa, typically without this having being realised (e.g., limestone cave reserves).

The conservation of rainforests is critical for molluscan conservation. They occupy only about 4.5% of Australian forests but contain a large proportion of the molluscan taxa. Existing rainforests are essentially refugia, occupying only about 20,000 km², mainly along the east coast of Australia (Webb and Tracey, 1981) with a few small areas of monsoonal rainforest patches from Cape York Peninsula in the north east to the Kimberley in the north west. Much of the lowland rainforest has been cleared for

agriculture. Rainforest remnants are still being cleared and are sometimes considered of little or no conservation value if they are of insufficient size to maintain large vertebrates. However, such areas may be vital for the continuing existence of locally endemic invertebrates, small plants and even small vertebrates (e.g., McEave et al., 1991).

The tropical rainforests of NE Queensland are a very important habitat for land snails (Stanisic, 1994) some locations with in excess of 40 species of land molluscs. Dry rainforest (vine thickets) inland from the coast in Queensland have reduced diversity (averaging about 10 species) although inland areas of moist refugia or limestone have higher diversities (Stanisic, 1994). The subtropical rainforests of south east Queensland and New South Wales also contain diverse molluscan faunas (Colman and Burch, 1977; Stanisic, 1994). Although generally a lower diversity than those further north (Stanisic, 1994), areas associated with limestones in the Macleay Valley peak in diversity at 36 species but in most sites in northern NSW 10–20 species is usual (Stanisic, 1994). There are few locations in the world in which the land mollusc diversity exceeds 30 species (Solem, 1984b). Monsoonal rainforests occur in small patches across northern Australia and are mostly poorly documented for molluscs but the Kimberley rainforest patches have been surveyed in some detail (McKenzie et al., 1991). These contain a rich molluscan fauna (Solem, 1991; Solem and McKenzie, 1991) with 115 species, all but 22 being camaenids. There is an average 12.5 species (average 3.7 species of camaenids) per rainforest patch (size <1 ha to > 20), the mean species range for camaenids was about 20 km in diameter and about 64% of camaenids were recorded from only one or two patches. Temperate rainforests, typically dominated by *Nothofagus*, are found in Victoria and Tasmania, although the great majority (456,000 ha) is in Tasmania. These forests also contain a distinctive fauna, but it is less diverse than that seen in northern rainforests.

The remaining 95.5% of Australian forests are mainly dry forests, much of this dominated by eucalypts (about 67.4%). Such forests are generally poor habitats for terrestrial molluscs, although wet sclerophyll (mixed eucalypt and rainforest species) can contain diverse faunas. Rainfall can be high in some areas with eucalypt forests but even in these areas molluscan faunas are typically sparse, probably because of generally low water retention in soils and regular fires.

However, dry forests can be important habitats when local topography or geology results in establishing suitable conditions for refugia.

Other terrestrial areas of high conservation value are largely circumscribed by geomorphological features resulting in their being very long-term suitable habitats. Of particular importance are limestone outcrops in which endemicity of terrestrial species is usually very high. This is especially true in eastern Queensland and New South Wales (Stanisic, 1994) and in north Western Australia (Solem, 1981a,b, 1984a, 1985, 1988, 1991). When limestone areas occur in rainforests diversity is particularly high (Stanisic, 1994). Limestone habitats are often protected, at least in part, if they are associated with caves. However, many other outcrops are not protected and are often cleared or mined.

Arid zone refugia, particularly deep gorges, can be very important, especially if associated with limestone. There is a rich camaenid fauna in the Kimberley (Solem, 1981a,b, 1984a, 1985, 1988, 1991), Flinders Ranges (Solem, 1992a,b), and the gorges of the Red Centre (Solem, 1993), and even the coastal areas along the Great Australian Bight have a few endemic species (Solem, 1992a,b). In an important review of arid zone refugia (Morton et al., 1995), published data on terrestrial and aquatic molluscs were taken into account. However, when assessing the relative conservation importance of particular habitats only threatened vertebrates (ANZECC listed species) were considered.

The conservation of Australian aquatic habitats is reviewed by Lake (1980) and McComb and Lake (1988). The only national review of the conservation of Australian inland aquatic fauna is that of Michaelis (1986), but few molluscs were noted. Most Australian lakes are very recent and do not contain endemic molluscan faunas. A few Tasmanian lakes, particularly Lake Sorell, Lake Crescent and Great Lake are older and contain a few endemics (Fulton, 1983), including some molluscan taxa. The few large rivers in Australia have a rather low diversity of freshwater molluscs when compared with some rivers in south east Asia and North America. The most conspicuous of the freshwater molluscs, the hyriids, are typically widely distributed, although *Hyridella glenelgensis* (south western Victoria) and *H. moretonicus* (Tasmania) are exceptions (McMichael and Hiscock, 1958).

Small streams and, to a lesser extent, local ground-water seepages and springs, are the major habitats of the majority of hydrobiid

there is virtually no information on the biology and ecology of most Australian non-marine molluscs. Such basic data gathering is vital to our understanding of how we might best facilitate the long term survival of many taxa. Coupled with this, work on the threats to native molluscs needs to be encouraged and facilitated. For example, there is virtually no data on the long term affects of fire, damming, salination and pollution on Australian molluscs.

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References

- Altena, C.O. van R. and Smith, B.J., 1975. Notes on introduced slugs of the families Limacidae and Milacidae in Australia, with two new records. *Journal of the Malacological Society of Australia* 3: 63–80.
- Baker, G.H., 1989. Damage, population dynamics, movement and control of pest helioid snails in southern Australia. pp. 175–185 in Henderson, I. (ed.) *BCPC Monogr. No. 41. Slugs and Snails in World Agriculture*.
- Butcher, R.J., P.E. Clunie, and A.L. Yen, 1994. The Victorian *Flora and Fauna Guarantee Act*: flagship legislation for invertebrate conservation. *Memoirs of the Queensland Museum* 36: 13–19.
- Butcher, R. and T.J. Doeg, 1995. Conservation of freshwater invertebrates. *Victorian Naturalist* 112: 15–19.
- Campbell, I.C. and T.J. Doeg, 1989. Impact of timber harvesting and production on streams: a review. *Australian Journal of Marine and Freshwater Research* 40: 519–539.
- Climo, F.M., 1981. Punctidae — minute land snails. P. 11 in: Recher, H.F. and Ponder, W.F., (eds). *Lord Howe Island, a summary of current and projected scientific and environmental activities. Occasional Reports of the Australian Museum* 1.
- Colman, P.H. and Burch, J.B., 1977. Molluscs. Pp. 54–58 in: Goldstein, W. (ed.), *Rainforests*. Reprinted from Parks and Wildlife. 2(1). National Parks and Wildlife Service, NSW.
- Cooling, M.P. and Boulton, A.J., 1993. Aspects of the hyporheic zone below the terminus of a South Australian arid-zone stream. *Australian Journal of Marine and Freshwater Research* 44: 411–426.
- Daniell, A., 1994. Genetics and terrestrial mollusc conservation. *Memoirs of the Queensland Museum* 36: 47–53.
- DEST, 1994. *Australia's biodiversity, an overview of selected significant components*. Biodiversity Series, Paper 2, Biodiversity Unit, Department of the Environment, Sport and Territories: Canberra. 87 pp.
- Evans, J.W., 1942. *The food of trout in Tasmania*. Salmon and Freshwater Fisheries Commission, Hobart.
- Fulton, W., 1983. Macrobenthic fauna of Great Lake, Arthurs Lake and Lake Sorell, Tasmania. *Australian Journal of Marine and Freshwater Research* 34: 775–785.
- Groombridge, B. (ed.), 1993. *1994 IUCN Red List of threatened animals*. IUCN, Gland., Switzerland and Cambridge, UK. Ivi + 286 pp.
- Habermehl, M.A., 1982. *Springs in the Great Artesian Basin, Australia — their origin and nature*. Australian Bureau of Mineral Resources, Geology and Geophysics, Report No. 235.
- Hart, B., 1993. A national approach to river management. *Search* 24: 125–130.
- Hill, A., Johnson, M.S. and Merrifield, H., 1983. An electrophoretic and morphological examination of *Bothriembryon kendricki* (Pulmonata: Bulimulidae), a new species previously considered conspecific with *B. bulla* (Menke). *Australian Journal of Zoology* 31: 227–242.
- Hutton, I., 1986. *Lord Howe Island*. Conservation Press: Canberra, 157 pp.
- Invertebrate Advisory Committee, 1994. *Interim list of native invertebrates which are threatened or rare in Tasmania*. Parks and Wildlife Service: Hobart. 44 pp.
- Iredale, T., 1944. The land Mollusca of Lord Howe Island. *Australian Zoologist* 10: 299–334.
- Iredale, T., 1945. The land Mollusca of Norfolk Island. *Australian Zoologist* 11: 46–71.
- Jackson, P.D., 1981. Trout introduced into south-eastern Australia: their interaction with native fishes. *Victorian Naturalist* 98: 18–24.
- Kershaw, R.C., 1991. *Snails and slugs introduced to or pests in Tasmania*. Queen Victoria Museum and Art Gallery, Launceston. 67 pp.
- Kuiper, J.G.J., 1983. The Sphaeriidae of Australia. *Basteria* 47: 3–52.
- Lake, P.S., 1980. Conservation. Pp. 163–173 in: Williams, W.D. (ed.), *An ecological basis for water resource management*. Australian National University Press: Canberra.
- Martin, P., and Lockie, S., 1993. Environmental information for total catchment management: incorporating local knowledge. *Australian Geographer* 24: 75–85.
- McComb, A.J., and Lake, P.S. (eds), 1988. *The conservation of Australian wetlands*. Surrey Beatty and Sons: Chipping Norton. 196 pp.
- McKenzie, N.L., Johnston, R.B. and Kendrick, P. G. (eds), 1991. *Kimberley rainforests of Australia*. Surrey Beatty and Sons: Chipping Norton. xiv + 490 pp.

- McMichael, D.F., and Hiscock, I.D., 1958. A monograph of the freshwater mussels (Mollusca: Pelecypoda) of the Australian region. *Australian Journal of Marine and Freshwater Research* 9: 372-508.
- Meave, J., Kellman, M., McDougall, A. and Rosales, J., 1991. Riparian habitats as tropical forest refugia. *Global Ecology and Biogeography Letters* 1: 69-76.
- Michaelis, F.B., 1984. Possible effects of forestry on inland waters of Tasmania: a review. *Environmental Conservation* 11: 331-344.
- Michaelis, F.B., 1986. Conservation of Australian aquatic fauna. Pp. 599-613 in: DeDeckker, P. and Williams, W.D. (eds), *Limnology in Australia*. CSIRO: Melbourne.
- Morton, S.R., Short, J. and Barker, R.D., 1995. *Refugia for biological diversity in arid and semi-arid Australia*. Biodiversity Series, Paper 4, Biodiversity Unit, Department of Environment, Sport and Territories. 171 pp.
- New, T.R., 1995. *Introduction to invertebrate conservation biology*. Oxford University Press: Oxford. xxi + 194 pp.
- Norris, R.H., Lake, P.S. and Swan, R., 1982. Ecological effects of mine effluents on the South Esk River, North-eastern Tasmania III. Benthic macroinvertebrates. *Australian Journal of Marine and Freshwater Research* 33: 789-809.
- Petterd, W.F., 1889. Contributions for a systematic catalogue of the aquatic shells of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 1888: 60-82, pls 1-4.
- Pollard, D.A., and Burchmore, J.J., 1986. A possible scenario for the future of Australia's freshwater fish fauna. Pp. 615-636 in: DeDeckker, P. and Williams, W.D. (eds), *Limnology in Australia*. CSIRO: Melbourne.
- Ponder, W.F., 1981a. Freshwater snails. P. 11 in: Recher, H.F. and Ponder, W.F. (eds), Lord Howe Island, a summary of current and projected scientific and environmental activities. *Occasional Reports of the Australian Museum* 1.
- Ponder, W.F., 1981b. *Posticobia norfolkensis* (Sykes), an apparently-extinct, freshwater snail from Norfolk Island (Gastropoda: Hydrobiidae). *Proceedings of the Linnean Society of NSW* 105: 17-21.
- Ponder, W.F., 1982. Hydrobiidae of Lord Howe Island (Mollusca: Gastropoda: Prosobranchia). *Australian Journal of Marine and Freshwater Research* 33:89-159.
- Ponder, W.F., 1986. Mound springs of the Great Artesian Basin. Pp. 403-420 in: DeDeckker, P. and Williams, W.D. (eds), *Limnology in Australia*. CSIRO: Melbourne.
- Ponder, W.F., 1992a. Bias and biodiversity. *Australian Zoologist* 28: 47-51.
- Ponder, W.F., 1992b. A new genus and species of aquatic cave-living snail from Tasmania (Mollusca: Gastropoda: Hydrobiidae). *Papers and Proceedings of the Royal Society of Tasmania* 126: 23-28.
- Ponder, W.F., 1994. Australian freshwater Mollusca: Conservation priorities and indicator species. *Memoirs of the Queensland Museum* 36: 191-196.
- Ponder, W.F. and Clark, G.A., 1990. A radiation of hydrobiid snails in threatened artesian springs in western Queensland. *Records of the Australian Museum* 42: 301-363.
- Ponder, W.F., Clark, G.A., Miller, A.C. and Toluzzi, A., 1993. On a major radiation of freshwater snails in Tasmania and eastern Victoria: A preliminary overview of the *Beddomeia* group (Mollusca: Gastropoda: Hydrobiidae). *Invertebrate Taxonomy* 7: 501-750.
- Ponder, W.F., Colgan, D.J., Clark, G.A., Miller, A.C. and Terzis, T., 1994. Microgeographic, genetic and geographical differentiation of freshwater snails — the Hydrobiidae of Wilsons Promontory, Victoria, south eastern Australia. *Australian Journal of Zoology* 42: 557-678.
- Ponder, W.F., Colgan, D.J., Terzis, T., Clark, S.A. and Miller, A.C., 1996. Three new morphologically and genetically determined species of hydrobiid gastropods from Dalhousie Springs, northern South Australia, with the description of a new genus. *Molluscan Research*, 17: 49-109.
- Ponder, W.F., Egger, P. and Colgan, D.J., 1995. Genetic differentiation of aquatic snails (Gastropoda: Hydrobiidae) from artesian springs in arid Australia. *Biological Journal of the Linnean Society* 56: 553-596.
- Ponder, W.F., Hershler, R. and Jenkins, B., 1989. An endemic radiation of hydrobiid snails from artesian springs in northern South Australia: their taxonomy, physiology, distribution and anatomy. *Malacologia* 31: 1-140.
- Ridge, S., 1995. *A study of how environmental parameters impinge on the disturbance and abundance of freshwater molluscs in the coastal drainages between Jervis Bay and Sydney*. Honours Thesis, University of Wollongong.
- Sheldon, F. and Walker, K.F., 1993a. Pipelines as a refuge for freshwater snails. *Regulated Rivers: Research and Management* 8: 295-299.
- Sheldon, F. and Walker, K.F., 1993b. Shell variation in Australian *Notopala* (Gastropoda: Prosobranchia: Viviparidae). *Journal of the Malacological Society of Australia* 1993: 59-71.
- Smith, B.J., 1981. Introduced non-marine molluscs in Australia. *Victorian Naturalist* 98: 24-27.
- Smith, B.J., 1992. Non-marine Mollusca. *Zoological Catalogue of Australia* 8: 1-398.
- Smith, B.J., and Kershaw, R.C., 1979. *A field guide to the non-marine molluscs of south eastern Australia*. Australian National University Press: Canberra. x + 285 pp.
- Smith, B.J. and Kershaw, R.C., 1981. *Tasmanian land and freshwater molluscs*. Fauna of Tasmania Handbook, 5. 148 pp.

- Smithers, C., McAlpine, D., Colman, P. and Gray, M., 1977. *Island invertebrates. Lord Howe Island*. Australian Museum: Sydney.
- Solem, A., 1981a. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley, *Amplirhagada* Iredale, 1933. *Records of the Western Australian Museum, Supplement* 11: 147–320.
- Solem, A., 1981b. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). III. Taxa from Ningbing Ranges and nearby areas. *Records of the Western Australian Museum, Supplement* 17: 427–705.
- Solem, A., 1984a. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley, *Westraltrachia* Iredale, 1933. *Records of the Western Australian Museum, Supplement* 11: 147–320.
- Solem, A., 1984b. A world model of land snail diversity and abundance. Pp. 6–22 in: Solem, A. and Van Bruggen, A.C. (eds), *World-wide snails*. Biogeographical studies on non-marine Mollusca. E.J. Brill/Dr W. Backhuys, Leiden.
- Solem, A., 1985. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley taxa and addenda to the Kimberley. *Records of the Western Australian Museum, Supplement* 20: 707–981.
- Solem, A., 1988. New camaenid land snails from the northeast Kimberley, Western Australia. *Journal of the Malacological Society of Australia* 9: 27–58.
- Solem, A., 1991. Land snails of Kimberley rainforest patches and biogeography of all Kimberley land snails. Pp. 145–246 in: McKenzie, N.L., Johnston, R.B. and Kendrick, P.G., (eds), *Kimberley rainforests of Australia*. Surrey Beatty and Sons: Chipping Norton.
- Solem, A., 1992a. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Part 1. Systematics, distribution, and variation. *Records of the South Australian Museum, Monograph Series* 2: 1–338.
- Solem, A., 1992b. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Part 2. Biogeography and covariation. *Records of the South Australian Museum, Monograph Series* 2: 339–395.
- Solem, A., 1993. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). VI. Taxa from the Red Centre. *Records of the Western Australian Museum, Supplement* 43: 983–1459.
- Solem, A. and McKenzie, N.L., 1991. The composition of land snail assemblages in Kimberley rainforests. Pp. 247–263 in: McKenzie, N.L., Johnston, R.B. and Kendrick, P.G., (eds), *Kimberley rainforests of Australia*. Surrey Beatty and Sons: Chipping Norton.
- Stanisic, J., 1981. Land Mollusca. Pp. 12–13 in: Recher, H.F. and Ponder, W.F. (eds), *Lord Howe Island, a summary of current and projected scientific and environmental activities. Occasional Reports of the Australian Museum* 1.
- Stanisic, J., 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum* 30: 1–241.
- Stanisic, J., 1994. The distribution and patterns of species diversity of land snails in eastern Australia. *Memoirs of the Queensland Museum* 36: 207–214.
- Stoddart, J.A., 1983. The accumulation of genetic variation in a parthenogenetic snail. *Evolution* 37: 546–554.
- Stoddart, J.A., 1985. Analysis of species lineages of some Australian thiarids (Thiaridae, Prosobranchia, Gastropoda) using the evolutionary species concept. *Journal of the Malacological Society of Australia* 7: 7–16.
- Tilzey, R.D.J., 1980. Introduced fish. Pp. 271–279 in: Williams, W.D. (ed), *An ecological basis for water resource management*. Australian National University Press: Canberra.
- Walker, K.F., 1985. A review of the ecological effects of river regulation in Australia. *Hydrobiologia* 125: 111–129.
- Walker, K.F., Thoms, M.C. and Sheldon, F., 1992. Effects of weirs on the littoral environment of the River Murray, South Australia. Pp. 270–293 in: Boon, P.J., Calow, P.A. and Petts G.E. (eds), *River Conservation and Management*. Wiley: Chichester.
- Webb, L.J. and Tracey, J.G., 1981. Rainforests: patterns and change. Pp. 606–694 in: Keast, A. (ed), *Ecological biogeography of Australia*. W. Junk, The Hague.
- Williams, W.D., 1980. Catchment management. Pp. 100–114 in: Williams, W.D. (ed), *An ecological basis for water resource management*. Australian National University Press: Canberra.
- Wilson, J.H., 1966. The food of trout in Great Lake. *Australian Society of Limnology, Newsletter* 5: 21–23.
- Woodruff, D.S. and Solem, A., 1990. Allozyme variation in the Australian camaenid land snail *Cristilabrum primum*: a prolegomenon for a molecular phylogeny of an extraordinary radiation in an isolated habitat. *The Veliger* 33: 129–139.
- Yen, A.L. and Butcher, R.J., 1992. Practical conservation of non-marine invertebrates. *Search* 23: 103–105.

A CONSERVATION PROGRAMME FOR THE PARTULID TREE SNAILS OF THE PACIFIC REGION

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Abstract

Pearce-Kelly, P., Clarke, D., Walker, C. and Atkin, P., 1997. A conservation programme for the partulid tree snails of the Pacific region. *Memoirs of the Museum of Victoria* 56(2): 431-433.

Throughout the Pacific numerous endemic mollusc species have either become extinct in the wild or are currently facing the threat of extinction as a result of introduction of the predatory snail *Euglandina rosea* and the New Guinea flatworm *Platydemus manokwari*. Without determined conservation efforts, including the establishment of *ex situ* breeding programmes, much of the region's endemic snail fauna will be lost. Since 1986 a collaborative international conservation programme has been in place for partulid tree snails. The participating institutions currently maintain a total of 33 taxa in culture (comprising > 12 000 snails). The conservation status of all 117 partulid species has been assessed using the *Conservation Action Management Plan* (CAMP) process. Target *ex situ* population sizes required to maintain 90% of starting heterozygosity over 100 years have been calculated using the analytical model programme CAPACITY (Pearce-Kelly et al., 1994). The genetic management requirements of the breeding programme have necessitated the development of a colony management computer database enabling demographic management and analysis of the populations. The ability of long term captive-bred snails to readapt to natural field conditions was investigated using a trial release and monitoring experiment at Kew Gardens. Field introduction trials via the construction of predator-proof forest reserves, were commenced in 1994.

Introduction

An ill-conceived attempt at biological control of the African land snail *Achatina fulica* (using the snail predator *Euglandina rosea* and the New Guinea flatworm *Platydemus manokwari*) has resulted in large numbers of endemic mollusc species becoming extinct, or facing the threat of extinction, throughout the Pacific region. Without the establishment of *ex situ* breeding programmes many of these endemic species will face extinction.

The 117 species of Polynesian tree snails of the family Partulidae once spread over a wide group of volcanic islands of the west, central and south Pacific. Each island had its own endemic species, which were often further restricted to individual valleys. The product of extraordinary selective pressures, *Partula* (the largest and most studied genus of the Partulidae) has provided researchers with an invaluable insight to the mechanisms behind speciation (Johnson et al., 1995). In addition to their scientific importance many species of Partulidae are valued elements of the region's rich cultural heritage.

The introduction of *Euglandina* has had a disastrous effect on the region's species of Partuli-

dae. *Euglandina* paid scant attention to its intended *Achatina* target preferring to prey on the smaller endemic snails. Extensive field surveys have determined that many partulid species have been preyed to extinction throughout their natural range (Murray and Clarke, 1984; Pearce-Kelly et al., 1994).

In 1986 the international zoo community, in association with IUCN's Captive Breeding Specialist Group, devised an international conservation programme to establish viable *ex situ* populations of as many endangered partulid species as possible. The programme is currently maintaining in culture 33 taxa (totalling >12 000 individuals) in 18 collections in Europe and North America.

A workshop in 1994 used the *Conservation Action Management Plan* (CAMP) process (Seal et al., 1994) to assess the conservation status of every species within the Partulidae. This review determined that no species could be considered as being less than endangered and identified 53 species as being in need of urgent captive-breeding assistance (Pearce-Kelly et al., 1994). Because of the intensive culture requirements associated with the Partulidae, together with the large number of species requiring captive-

breeding assistance, the workshop calculated the target population sizes required to maintain 90% of starting heterozygosity over 100 years using the analytical model programme CAPACITY (Flesness and Mace, 1988; Soule et al., 1986). The results of this exercise suggested that a minimum of 250 adults, together with their associated young, need to be maintained for each species in the breeding programme.

The demographic labyrinth

Maintaining healthy genetic populations of any species over successive generations requires a management protocol that takes account of the major factors that lead to loss of genetic diversity. These factors are genetic drift (the random process which results when a limited sample of genes from one generation is transmitted to the next), inbreeding depression (mating between relatives which can result in reduced characters such as fertility and growth rate), artificial selection (the disproportionate survival of individuals adapted to the prevailing environmental conditions — in captivity selective pressures may differ from those in the wild) and disease. In order to balance these considerations the snail cultures are maintained along inbred and outbred lines with genetic drift and inbreeding depression being minimised in the outbred lines while the inbred lines best reduce the risks of selection pressures and disease.

The taxa in the Partulidae programme derive not only from different islands but from different valleys and collection sites within valleys. Each of the > 100 collection sites represents a genetically unique population which needs to be maintained as a separate breeding line. The need for generation separation and monitoring of the four developmental stages (defined as new born, juvenile, subadult and adult) are further management complications. These considerations are compounded by the need to maintain populations as colonies of up to 200 snails, of mixed age structure. The development of a computerized colony database (CERCI) has, for the first time, enabled the detailed monitoring and analysis of demographic trends, and environmental and genealogical data in colony populations.

Re-establishment

The effectiveness of the breeding programme in maintaining viable populations was tested in 1994 when a group of zoo-bred *Partula taeniata* was released on to Polynesian plants growing at

Kew Gardens. This 16 month trial suggested that long term captive-bred *Partula* populations have retained their ability to readapt to a natural environment and diet (Pearce-Kelly et al., 1995). The latest development has been the commencement of reestablishment on the French Polynesian island of Moorea (Murray, 1995). Because of continued predator threat, this aspect of the programme has involved the construction of a predator-proof reserve, 20 m × 20 m, built with cheap locally available materials, and containing three species of captive-bred *Partula* snails (Murray, 1995).

For the foreseeable future, it is not possible to progress beyond the predator-proof reserve strategy due to the high numbers of surviving *Euglandina* in the habitat. These *Euglandina* are feeding on native micro-snails in the leaf litter and will continue to prevent the full re-establishment of *Partula* into the wild until effective predator control measures are developed.

To ensure that the captive snails do not become diseased, lose their natural resilience to endemic micro-organisms, or introduce alien microbes when returned to their native habitat, an extensive screening exercise is in place to determine the nature and levels of enteric gut fauna and flora in both the wild and captive *Partula* populations.

Other conservation initiatives

Educational material is being produced to help raise public awareness of the ecological disaster facing the indigenous snail fauna throughout the Pacific and, to illustrate how Polynesians can help prevent further extinctions of endemic molluscs, legislation is being formulated to prohibit further introduction of alien species into French Polynesia. These two initiatives are the most effective conservation action that can be taken to reduce the likelihood of alien predators being introduced to islands that have thus far escaped such disastrous importations.

Conclusion

The extinction of endemic species of mollusc throughout the Pacific is continuing. Without concerted *in situ* and *ex situ* action, of the nature outlined above, it can only escalate. The significance for conservation of such action is highlighted by the number of species currently afforded a second chance of survival through captive-breeding programmes. In addition to benefiting the individual target species, such programmes are potential conservation models

for many of the more than 1000 IUCN-listed threatened mollusc species.

References

- Fleness, N. and Mace, G., 1988. Population databases and zoological conservation. *International Zoo Yearbook* 27: 44–49.
- Johnson, M.S., Murray, J. and Clarke, B.C., 1993. The ecological genetics and adaptive radiation of *Partula* on Moorea. *Oxford Surveys in Evolutionary Biology* 9: 167–238.
- Murray, J. and Clarke, B., 1984. Movement and gene flow in *Partula taeniata*. *Malacologia* 25: 343–348.
- Murray, J., 1995. *Conservation of Pacific land snails: Monitoring and rescue of endangered species*. A preliminary report to Flora and Fauna International, Cambridge, UK.
- Pearce-Kelly, P., Clarke, D. and Mace, G.M., 1994. *Partula '94: An action plan for the conservation of the family Partulidae*. Zoological Society of London: London.
- Pearce-Kelly, P., Mace, G. and Clarke, D., 1995. The release of captive bred snails (*Partula taeniata*) into a semi-natural environment. *Biodiversity and Conservation* 4: 645–663.
- Seal, U.S., Foose, T.J. and Ellis, S., 1994. Conservation assessment and management plans (CAMPS) and Global captive action plans. Pp. 312–328 in: Olney, P.J., Mace, G.M. and Feistner, A.T.C. (eds), *Creative conservation*. Chapman and Hall: London.
- Soule, M.E., Gilpin, M., Conway, W. and Foose, T., 1986. The millennium ark, how long a voyage, how many state rooms, how many passengers? *Zoo Biology* 5: 101–113.

DIVERSITY IN CENTRAL AUSTRALIAN LAND SNAILS (GASTROPODA: PULMONATA)

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Abstract

Scott, B., 1997. Diversity in central Australian land snails (Gastropoda: Pulmonata). *Memoirs of the Museum of Victoria* 56(2): 435-439.

Much of the land snail diversity in central Australia is due to camaenids (70 of 83 spp.). Many camaenid species have restricted distributional ranges so that, although land snail diversity in Central Australia is relatively high, local diversity is generally low. The fauna of the Krichauff Range in the Central Ranges is an exception to this general rule as the Finke Gorge National Park contains at least 25 species of snails, 30% of the central Australian fauna. Similar areas in the Central Ranges, such as the George Gill Range and eastern MacDonnell Ranges have a significantly lower diversity of land snails. It is postulated that high levels of diversity and endemism in central Australian camaenids are the product of vicariance events related to Tertiary and Quaternary changes in climate.

Introduction

Over 80 species of land snails from eight families have been recorded from central Australia (Solem, 1989, 1991, 1993; Scott, in prep.). The land snail fauna is dominated by the families Camaenidae and Pupillidae *s.l.*, both of which are widespread across mainland Australia. Other families are represented in this area by no more than two species each. It has been suggested that the relatively small number of families in the central Australian fauna (compared with the greater complement in coastal areas) is the result of dispersal from coastal centres of origin to the interior, combined with the effect of filtering due to fluctuating climatic conditions (Solem, 1993). Problems arise, however, with dispersal hypotheses as explanations of the origin and distribution of organisms as they are *ad hoc* narratives used to describe specific cases and, as such, are generally untestable.

Hypotheses concerning vicariance biogeography provide alternative interpretations of distributions. In that model of historical biogeography, it is assumed that taxa and the areas they occupy have evolved together (Nelson and Platnick, 1981). Reconstruction of a phylogeny allows the reconstruction of the history of a region. Biogeographic hypotheses erected using data from one group of organisms can be tested with those from another. Land snails are excellent subjects for such biogeographic studies as they are 'vicariant conformers' (Springer, 1981: 230), responding rapidly to environmental disruptions (Gould, 1969).

Origins and diversification of the Central Australian land snail fauna

It has been suggested that many families represented in central Australia were Tertiary invaders from Asia and that the apparent reduction in diversity from north to south and from east to west is a result of dispersal from tropical centres of origin (Solem, 1959, 1992, 1993). The most diverse of those families, the Camaenidae, is postulated to have entered Australia in several waves (Solem, 1959, 1992, 1993; Bishop, 1981), the products of the earliest wave having the most extensive distribution and those of the most recent restricted to the eastern rainforests (Solem, 1959). This interpretation is based on the assumption of monophyly of American and Australasian camaenids but this assumption is probably incorrect (Scott, 1996). It is possible that the Australasian component of this family is closely related to the Asian Bradybaenidae (Scott, 1996) and is of Gondwanan origin (Scott, in press).

Central Australian camaenids show a high degree of regional endemism but two genera in the subfamily Sinumeloninae, *Sinumelon* and *Pleuroxia*, have ranges that extend beyond the Centre. Species of these genera occur in the Centre and in southern and parts of western Australia (Solem, 1992, 1993). This has been interpreted as the result of primary differentiation of ancestral taxa in the Centre, followed by southerly and westerly migrations to give rise to local radiations (Solem, 1992, 1993). Present distributions may, however, also be explained as the result of tectonic or climate-induced vicar-

iance events which caused populations of ancestral taxa to become isolated and thus to give rise to modern taxa. Preliminary studies on the phylogeny and cladistic biogeography of the Sinumeloninae indicate that fauna of southern and western coastal areas was separated from that of central Australia early in the evolutionary history of the group (Scott, in prep.). Within the central Australian region, some montane areas, such as the Central Ranges, may have become isolated from adjacent areas not long after the Centre-SW split. Vicariance events causing disruptions of these magnitudes may have been associated with cyclical climate change in the Cenozoic, when periods of relative dryness associated with global cooling alternated with warm and humid pluvial stages. Alternation of arid grasslands and extensive water bodies in the plains and valleys may have presented significant barriers to formerly widespread snail taxa. Which of the two extremes may have played the more significant role cannot be determined, but they may have acted synergistically.

Congeners of the central Australian bulimulid *Bothriembryon spenceri* (Tate, 1894) are found in southern and western parts of the continent, as well as the south-eastern coast of Tasmania (Smith, 1992). There is generally little spatial overlap between the Camaenidae and Bulimulidae as camaenids do not occur in Tasmania or the extreme south-west of the mainland and *Bothriembryon* is not found in the north or east. However, although the distributions of *Bothriembryon* and the two camaenid genera, *Sinumelon* and *Pleuroxia*, do not correspond entirely, broad geographical congruence between the three genera is such that future phylogenetic and biogeographic analysis of one genus will provide a hypothesis available for testing with the other two genera.

Patterns of diversity in the Central Ranges land snail fauna

Almost half of the Central Australian species of land snail have been recorded from the Central Ranges (MacDonnell, Krichauff and George Gill Ranges) (Smith, 1992; Solem, 1993; Scott, in prep.), which cover 12% of the area of this region, while Finke Gorge, in the Krichauff Range, alone contains almost a third of the central Australian land snail species (Table 1). The snail fauna of the Central Ranges is well-known as collecting sites are readily accessible, but direct comparison between the Central Ranges and adjacent areas may present problems as sites

further away from Alice Springs may have been less thoroughly explored.

Camaenid species comprise 66% of the land snail fauna of the Central Ranges and demonstrate a high level of endemism compared with species in other families (Table 2). The non-camaenid species of that fauna are largely widespread, shared with other parts of Central Australia and, in several cases, also with coastal areas.

The pattern of diversity demonstrated by camaenids in the Central Ranges can be seen in other areas such as the Kimberley and adjacent ranges (Solem, 1979, 1981a, 1981b, 1984b, 1985, 1988a, 1989). Many of these endemic species have narrow ranges which are usually allopatric to congeners (Solem, 1988b). This appears to be a common pattern among land snails (Solem, 1984c) and it is rare for two short-range Central Ranges endemics to occur sympatrically, although they are frequently found with other more widely-distributed species. Geographic ranges do not appear to be restricted by competition as they are never parapatric and, as narrow-range endemics do not come into contact with each other, there can be no evidence of repressive interactions.

Pleuroxia adcockiana (Bednall, 1894) is the sole representative of the genus in the Central Ranges and the edges of its distribution coincide with those of the Central Ranges biogeographical area. The four species of *Sinumelon* in this area are moderate-range endemics and divide the Central Ranges into four units: far western MacDonnell Ranges, Krichauff and James Ranges (*S. expositum* Iredale, 1937), near western MacDonnell Range and Alice Springs (*S. bednalli* Ponsonby, 1904), eastern MacDonnell Range (*S. dulciensis* Solem, 1993) and George Gill Range (*S. gillensis* Solem, 1993) (Solem, 1993).

The genera *Granulomelon* and *Semotrachia* show very high degrees of endemism. Three of five species of *Granulomelon* are found in the Central Ranges and two of those are known only from single localities, at opposite ends of Finke Gorge (Solem, 1993; Scott, in prep.). *Semotrachia* is an extremely diverse genus, with 18 of its 28 species known only from the Central Ranges (Solem, 1992; Scott, in prep.). Many (16) of these species are narrow-range endemics, confined to single gorges in the eastern and western MacDonnell Ranges, or from rock walls in the Krichauff, James and George Gill Ranges.

Combination of patterns of distribution from these species suggests that although the Central

Table 1. Land snail diversity in Central Ranges (data compiled from Solem, 1989, 1991, 1993; Scott, in prep.) (^a total number of species recorded from the Central Ranges = 39; ^b total number of species recorded from central Australia = 83).

	No. of species ^a	% of species recorded from central Australia ^b
Western MacDonnell Range	23	27.7
Eastern MacDonnell Range	14	16.8
Krichauff and James Ranges	27	32.5
Finke Gorge	25	30.1
George Gill Range	9	10.8

Table 2. Land snail diversity at selected sites in the Central Ranges (sites are approximately equivalent in size) (data compiled from Solem, 1984a, 1989, 1991, 1993; Scott, in prep.)

	endemic camaenids	non-endemic camaenids	endemic others	non-endemic others
Krichauff Range				
Finke Gorge	7	4	0	14
W MacDonnell Range				
Glen Helen	1	3	0	12
Serpentine Gorge — Ellery Big Hole	1	3	0	5
Simpson Gap — Fenn Gap	2	3	0	6
Alice Springs	1	3	0	6
Eastern MacDonnell Range	4	4	0	6
George Gill Range	2	0	1	6

Ranges represent a coherent biogeographic unit, this unit can be divided into seven areas, each with its own evolutionary history. The Alice Springs region, eastern MacDonnell Ranges, Krichauff and James Ranges, and the George Gill Range each represent single areas, while the western MacDonnell Range is a composite of three sub-areas.

Evolution in the Central Ranges

The Central Ranges are subparallel strike ridges, running approximately east-west, and are composed principally of sandstone and quartzite with some dolomite and shale (Mabbutt, 1967; Thompson, 1991). The MacDonnell Ranges are divided into eastern and western components by the Todd River and the western range is separated from the Krichauff and James Ranges immediately to its south by Missionary Plain. The Krichauff and James Ranges are continuous with the eastern MacDonnell Range as one arm of a geosyncline; the western MacDonnell Range forms the other arm (Thompson, 1981).

Extreme climate changes of the Tertiary are registered in the geomorphology of the Central Ranges. The ranges rise abruptly from plains and, in many areas, are capped with duricrust, indicating the pre-erosional valley floors of the Tertiary. Exposure of the mountain ranges and the subsequent cutting of gorges through the ranges has probably occurred only over the last 20 million years (Twidale, 1994). The presence of numerous watercourses, which cut across the ranges rather than run parallel to them, indicate the importance of water in producing this landscape. Several significant waterways are found in this area, including the Finke River and its tributaries in the western MacDonnell and Krichauff Ranges, and the Ross River in the eastern MacDonnell Range.

Coincidence of waterways with the limits of biogeographic areas suggests that rivers may have been important in the dissection and isolation of ancestral populations. Water-cut gorges and depositional plains provide evidence of significant pluvial phases, during which snails might have been restricted to montane islands.

Increasing aridity during glacial phases may have contributed to the isolation of populations and subsequent speciation (e.g. Haffer, 1982; Winter, 1988; Bush and Colinvaux, 1990) but the numerous short-range endemic land snails in otherwise contiguous mountain ranges suggest that it is the presence of water, rather than its absence, which is the most important factor in speciation here.

Implications for land snail conservation

Short-range endemic invertebrates are often neglected when areas are selected for conservation. Economic imperatives ensure that surveys focus on readily-observed and readily-identified taxa, such as vascular plants and vertebrates with little attention directed towards other organisms. As the range of a snail species may be less than 0.5 km² (Solem, 1988b), the inclusion of narrow-range invertebrate taxa in protected areas is as likely to be the result of good luck as it is of good planning. Awareness of the possible existence of such taxa combined with an understanding of the history of an area will greatly increase the chances of short-range endemics being located and subsequently protected from extinction.

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References

Bishop, M.J., 1981. The biogeography and evolution of Australian land snails. Pp. 925–954 in: Keast, A. (ed.), *Ecological biogeography of Australia*. Dr W. Junk: The Hague.

Bush, M.B. and Colinvaux, P.A., 1990. A long climatic and vegetation record from lowland Panama. *Journal of Vegetation Science* 1: 105–118.

Gould, S.J., 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P.*

(*Poecilozonites*) in Bermuda. *Bulletin of the Museum of Comparative Zoology, Harvard* 138: 407–531.

Haffer, J., 1982. General aspects of the refuge theory. Pp. 6–24 in: Prance, T.G. (ed.), *Biological diversity in the tropics*. Columbia University Press: New York.

Mabbutt, J.A., 1967. Denudation chronology in central Australia: structure, climate and landform inheritance in the Alice Springs area. Pp. 144–181 in: Jennings, J.N. and Mabbutt, J.A. (eds), *Landform studies from Australia and New Guinea*. Australian National University Press: Canberra.

Nelson, G. and Platnick, N.I., 1981. *Systematics and biogeography: cladistics and vicariance*. Columbia University Press: New York.

Scott, B.J., 1996. Phylogenetic relationships of the Camaenidae (Gastropoda: Pulmonata: Stylommatophora). *Journal of Molluscan Studies* 62: 65–73.

Scott, B.J., in press. Biogeography of the Helicoidea, land snails with a Pangean distribution. *Journal of Biogeography*.

Smith, B.J., 1992. Non-marine Mollusca. *Zoological Catalogue of Australia* 8. Australian Government Publishing Service: Canberra.

Solem, A., 1959. Systematics and zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana, Zoology* 43: 1–359.

Solem, A., 1961. New Caledonian land and freshwater snails: an annotated checklist. *Fieldiana, Zoology* 41: 413–501.

Solem, A., 1979. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). I. Taxa with trans-Australian distribution. *Records of the Western Australian Museum, Supplement* 10: 1–142.

Solem, A., 1981a. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley. *Amplirhagada Iredale, 1933. Records of the Western Australian Museum, Supplement* 11: 147–320.

Solem, A., 1981b. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). III. Taxa from the Ningbing Ranges and nearby areas. *Records of the Western Australian Museum, Supplement* 11: 321–425.

Solem, A., 1984a. Small land snails from northern Australia. III. Species of Helicodiscidae and Charopidae. *Journal of the Malacological Society of Australia*, 6: 157–179.

Solem, A., 1984b. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley. *Westrachia Iredale, 1933. Records of the Western Australian Museum, Supplement* 17: 427–705.

Solem, A., 1984c. A world model of land snail diversity and abundance. Pp. 6–22 in: A. Solem and A.C. van Bruggen (eds), *World-wide snails: biogeographical studies on non-marine Mollusca*. E.J. Brill/Dr W. Backhuys: Leiden.

- Solem, A., 1985. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley taxa and addenda to the Kimberley. *Records of the Western Australian Museum, Supplement* 20: 707-981.
- Solem, A., 1988a. New camaenid land snails from the north-east Kimberley, Western Australia. *Journal of the Malacological Society of Australia* 9: 27-58.
- Solem, A., 1988b. Maximum in the minimum: biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, northeast Kimberley, Western Australia. *Journal of the Malacological Society of Australia* 9: 59-113.
- Solem, A., 1989. Non-camaenid land snails of the Kimberley and Northern territory, Australia. I. Systematics, affinities and ranges. *Invertebrate Taxonomy* 2: 455-604.
- Solem, A., 1991. Distribution and diversity patterns of Australian pupillid land snails (Mollusca: Pulmonata: Pupillidae, s.l.). *Veliger* 34: 233-252.
- Solem, A., 1992. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. *Records of the South Australian Museum, Monograph series* 2: 1-325.
- Solem, A., 1993. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae) VI. Taxa from the Red Centre. *Records of the Western Australian Museum, Supplement no. 43*: 983-1459.
- Springer, V.G., 1981. Comments on Solem's land snail biogeography, with an hypothesized explanation of the distribution of the Endodontidae. Pp. 225-230 in: Nelson, G. and Rosen, D.E. (eds), *Vicariance biogeography: a critique*. Columbia University Press: New York.
- Thompson, R.B., 1991. *A guide to the geology and landforms of central Australia*. Northern Territory Geological Survey: Alice Springs.
- Twidale, C.R., 1994. Gondwanan (Late Jurassic and Cretaceous) palaeosurfaces of the Australian craton. *Palaeogeography, Palaeoclimatology, Palaeoecology* 112: 157-186.
- Winter, J.W., 1988. Ecological specialization of mammals in Australia tropical and sub-tropical rainforest: refugial or ecological determinism. *Proceedings of the Ecological Society of Australia* 15: 127-38.

AN AREA OF EXCEPTIONAL LAND SNAIL DIVERSITY: THE MACLEAY VALLEY, NORTH-EASTERN NEW SOUTH WALES

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Abstract

Stanisic, J., 1997. An area of exceptional land snail diversity: the Macleay Valley, north-eastern New South Wales. *Memoirs of the Museum of Victoria* 56(2): 441–448.

In the Macleay Valley region, north-eastern New South Wales, the combination of rainforest and limestone has provided a unique environment for the evolution of a quite remarkable land snail fauna. 108 native species have been recorded in an area approximately bounded by the Nambucca River in the north, the Hastings River in the south and the eastern escarpment of the Great Dividing Range in the west. Much of this diversity is centred on a series of limestone exposures which outcrop in an east-west direction from just west of Kempsey to the ranges of the Werrikimbe National Park. Diversity levels on the limestones are high with 39 species of land snails recorded at an outcrop near Yessabah. In contrast rainforest sites have smaller numbers of species. Comparatively few species inhabit the sclerophyll forests. A number of species are endemic to the limestones and some of these exhibit specialised microhabitat preferences. This study examines the distribution of these species within the Macleay Valley region and elsewhere, and attempts to explain the development of this fauna in terms of past climate-induced changes in vegetation communities within the region. The implications of these findings for land snail conservation are discussed.

Introduction

The Macleay Valley in north-eastern New South Wales is an area of exceptional land snail diversity. Stanisic (1994) briefly discussed the significance of this region in an overview of land snail distribution in eastern Australia. Reasons for this concentration of terrestrial molluscs fauna in such a comparatively small area were linked to the co-occurrence of two significant land snail habitats — rainforest and limestone. Rainforest in the region is a complex mixture of a variety of structural types, and the limestone, as a series of isolated outcrops, is extensive and geographically unusual. In New South Wales, limestone outcrops occur mainly along the central and western parts of the Great Dividing Range from the Queensland to Victorian borders. The limestone outcrops of the Macleay Valley are unique in that they occur east of the Great Divide.

Moisture is critical for the survival of land snails. Because areas of rainforest are indicative of long term moisture stability it is not surprising that significant snail communities live in the rainforests of eastern Australia (Bishop, 1981; Smith, 1984; Stanisic, 1994). However the influence of limestone on the distribution of land snails in eastern Australia is largely undocumented. Stanisic (1990) described new Charopidae from outcrops in the Macleay Valley and

discussed the refugial nature of limestone habitats.

This study focusses on the land snails of the Macleay Valley region and specifically examines the significance of both rainforest and limestone outcrops in relation to their distribution within this area.

Study area

The Macleay Valley is situated west of the township of Kempsey, NSW. The study area is approximately bounded by the Nambucca and Hastings Rivers (in the north and south respectively) and the coastline and the Great Escarpment (in the east and west respectively). Collecting sites are confined within 30°30'–31°30'S and 152°00'–153°00'E (Fig. 1).

Rainfall in the region is generally non-seasonal (Nix, 1981) but highly variable. Mean annual rainfall is 1000–2000 mm but may exceed 3500 mm on some of the highest peaks where cool temperate rainforest occurs. In the lowlands and foothills, areas of dry rainforest receive 630–1100 mm and are characterised by a markedly seasonal climate.

The region supports a diverse array of vegetation communities including several distinct rainforest structural types (Fig. 2). On the coast, littoral rainforest, sometimes mingled with sub-

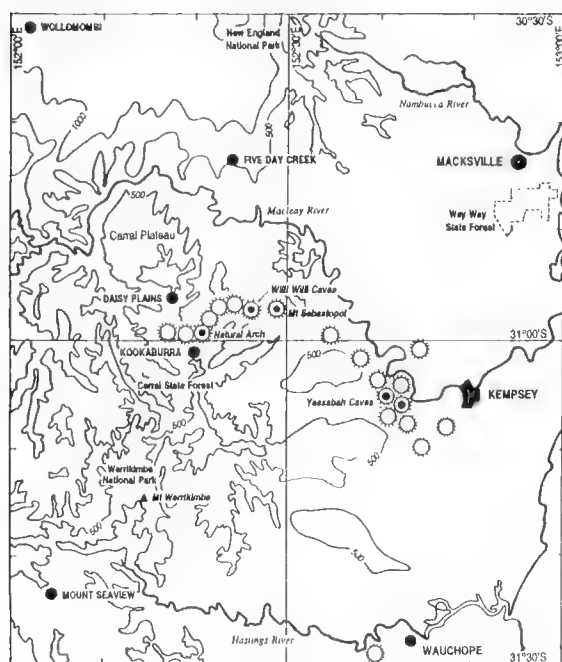


Figure 1. Study area. Limestone outcrops represented by spiked circles.

tropical rainforest, e.g. Sea Acres Nature Reserve ($31^{\circ}27'S$, $152^{\circ}55'E$), occurs among drier sclerophyllous communities. Open woodland communities, often largely cleared for farming dominate the less populated lowlands. In lowland areas where rainfall is high due to local topographic effects, subtropical rainforest flourishes e.g. Way Way State Forest ($30^{\circ}47'S$, $152^{\circ}56'E$) and Wilson River Primitive Reserve (Fig. 2A. $31^{\circ}12'S$, $152^{\circ}28'E$). Along water courses, e.g., Maria River ($31^{\circ}08'S$, $152^{\circ}49'E$), riverine rainforest provides important corridor habitat. On wetter slopes of the foothills of the Great Divide, wet sclerophyll forest alternates with dry sclerophyll and dry rainforest. The latter forest type is characterised a number of deciduous and semi-deciduous tree species and is a feature of the region (Floyd, 1983). In spite of the fact that these forests are comparatively depauperate floristically, their presence indicates a higher and more stable moisture regime than that available to nearby sclerophyll forest communities. Often this rainforest type is found growing on rock outcrops (limestone and volcanic) which not only act as sinks for available moisture but also as local fire shadows. There is an ample litter layer to provide considerable living spaces for land snails. Large stands of dry rainforest are located on the mid-slopes of Mt

Seaview (Fig. 2D. $31^{\circ}24'S$, $152^{\circ}15'E$), west of Wauchope (Floyd, 1980), and in the upper Macleay River valley on the Bellbrook-Wollomombi Rd ($30^{\circ}45'S$, $152^{\circ}22'E$). Most of the limestone outcrops in the region are covered in this type of vegetation. On the upper slopes and plateaux of the western ranges, warm temperate rainforest dominates. Much of this has been logged in the past (Adam, 1987) but reasonable stands are still present in such places as the Carrai Plateau ($30^{\circ}55'S$, $152^{\circ}17'E$), Fenwicks Flora Reserve (Fig. 2B. $31^{\circ}17'S$, $152^{\circ}08'E$) and Werrikimbe National Park ($31^{\circ}14'S$, $152^{\circ}17'E$). On the very tops of the highest peaks e.g. Banda Banda Flora Reserve ($31^{\circ}09'S$, $152^{\circ}25'E$), small stands of cool temperate rainforest, dominated by *Nothofagus moorei*, occur. The limestones of the Macleay Valley (Fig. 1) occur as an archipelago of outcrops from near Sherwood, just west of Kempsey, in a west-northwest direction to Stockyard Creek in the Werrikimbe National Park (Lishmund et al., 1986). Those in the lower Macleay River valley, e.g., Yessabah ($31^{\circ}05'S$, $152^{\circ}41'E$), Sherwood ($31^{\circ}03'S$, $152^{\circ}41'E$), are situated amidst dry woodland and support islands of dry rainforest. The limestone rock traps moisture and allows rainforest species to persist in otherwise inhospitable countryside. In contrast some of the more westerly outcrops are located among stands of dense rainforest, e.g., The Castles (Fig. 2C. $30^{\circ}59'S$, $152^{\circ}19'E$). Some of the outcrops are only very low exposures but the majority are substantial karst towers. In all cases their occurrence signals a dramatic change in vegetation and land snail fauna to that of the surrounding forests, especially when they occur in the drier woodland landscape.

In both of these main habitat types, i.e., rainforest and rainforest with limestone, land snails are favoured by a number of environmental factors which are not part of the sclerophyllous forest habitat profile. The ecologic factors which favour rainforest e.g. moisture and eutrophic soils are also those which favour the success of terrestrial molluscs. In addition rainforest provides ample food and shelter for snails (Bishop, 1981). Of particular importance to the snails is the accumulated litter and debris which characterise the forest floor of rainforests and provides a wide array of living spaces. Limestone outcrops, with their vegetative cloak of rainforest, are able to provide similar benefits for land snails with the added bonus of a ready supply of calcium for shell production. The complex array of cracks and holes which are a feature of limestone outcrops (Fig. 2E) enhance the matrix of

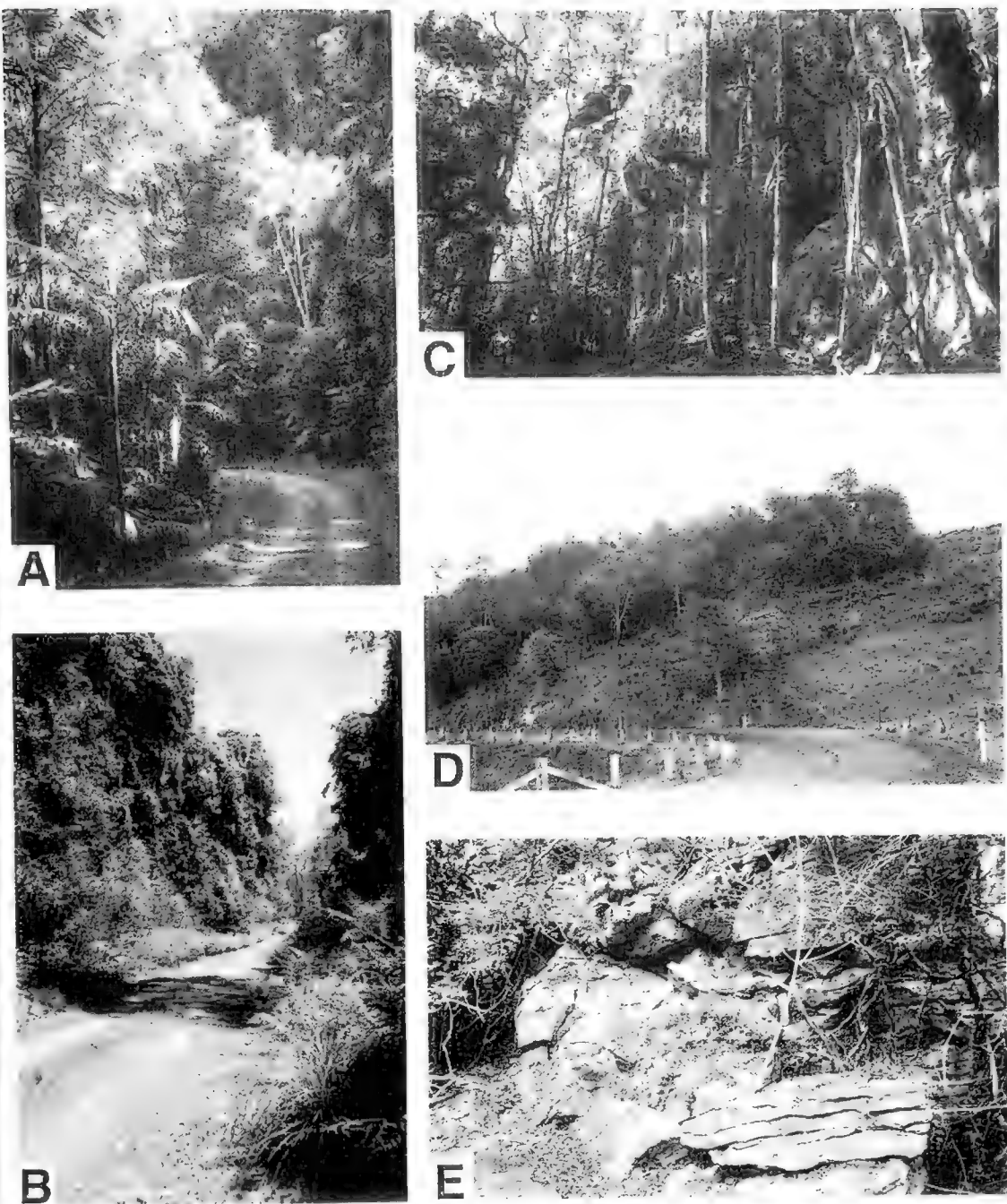


Figure 2. Land snail habitats in the study area. A, subtropical rainforest, Wilsons River Primitive Reserve; B, warm temperate rainforest, Fenwicks Flora Reserve; C, The Castles; D, dry rainforest, Mt Seaview Nature Reserve; E, microtopography of limestone habitat at Yessabah.

microhabitat types available for exploitation as living space.

Sampling methodology

Preliminary sampling of the area by the author began in 1987 but intensified in 1992 as part of a wider study to examine the charopid land snail fauna of limestone outcrops in eastern New South Wales. Eighty-five sites are included in the data set of localities used in this study. Each site is uniquely defined by a combination of latitude, longitude, altitude and a habitat descriptor which is vegetation-based. Of these, thirteen represent casual collecting, largely by non-specialist personnel. The majority (72) have involved the author and were sampled according to a systematic protocol. Many sites within the study area have been visited on more than one occasion.

Snails were hand collected and a quantity of leaf litter was taken from each site for sorting by microscope. Because snails lend themselves to 'post-mortem' sampling, litter sorting is an effective method for determining the presence or absence of species. This is particularly critical in a study such as this in which small snails (< 5 mm shell diameter or height) form the greater proportion of species present. All specimens were identified to species using both shell and animal characters by the author.

Results

The data set of examined material consists of 10 285 specimens belonging to 111 species. Of these, three species are introductions and are not included in the analyses. The remaining 108 species (69 undescribed) belong to 14 families. Species diversity is not evenly spread across families (Fig. 3). The largely litter-dwelling, tiny-shelled Charopidae is by far the most speciose with 53 species. Preliminary taxonomic studies show that this charopid diversity is only partially due to local radiations. There is however evidence of vicariant species. The charopid *Letomola contortus* (Hedley, 1924), from the Yessabah-Sherwood limestones, has an undescribed sister species in the more westerly Mt Sebastopol-Castles limestone blocks. Similarly the charopid *Coenocharopa yessabahensis* (Stanisic, 1990), from Yessabah has a sister species in the dry rainforests of the Mt Seaview area. The larger-shelled Camaenidae are next most diverse with 17 species represented including a significant local radiation of 'chloritids'

(Fig. 6C) which show parapatric distributions in the dry rainforest-sclerophyll forest complex. A number of new species of helicarionid semislugs (Fig. 6E) including the large *Parmavitrina planilabris* (Cox, 1866) (Fig. 6D) are features of the snail fauna. Some carnivorous rhytidids (Fig. 6F) are also endemic to the region.

Numbers of species per site (Fig. 4) varied markedly. Sites which included limestone recorded the highest numbers of species. The large outcrops at Yessabah (39 species), Natural Arch (34 species) and Mt Sebastopol (32 species) yielded the most species per site. However, even the smaller outcrops yielded relatively high numbers of species e.g. West of Sherwood (23) and south of the Willi Willi Rd (23). In comparison the best rainforest sites were in subtropical rainforest at the Pines rest area, Way Way State Forest and dry rainforest on the Wollomombi Rd in the upper Macleay River valley where 20 species were recorded. Other notable rainforest sites were the Mt Seaview Nature Reserve (18 species) and Fenwicks Flora Reserve (16 species). Cool temperate rainforest sites were comparatively impoverished (7–10 species). In contrast the sclerophyll sites all registered less than 10 species with many sites recording less than 5 species. These figures are not absolute and should be regarded only as indicators of site richness. The patchy nature of snail distribution in the natural environment (Stanisic, pers. obs.) makes it highly likely that additional species will be discovered in the region.

Examination of species distributions within broad habitat types shows that the limestone/rainforest biotope (10 sites) supports 67 species throughout the study region. Sites with rainforest alone (47) account for 85 of the species. Sites classified as dry and wet sclerophyll forest and including partially cleared woodland (28) were comparatively depauperate with only 31 species represented. If the rainforest/limestone biotope is considered as part of the rainforest habitat then 105 of 108 species are living in closed forests. Dry rainforest sites, including those with limestone support 71 species.

The insular nature of the region's land snail fauna is evident in the analysis of the species distribution profiles (Fig. 5). Forty-eight species occur only within the study area. Most of these belong to the Charopidae (32 species) which are very small and presumably less able to disperse. However, somewhat surprisingly, there are also a significant number of larger Camaenidae (9 species) endemic to the region. In the case of the

NUMBERS OF SPECIES

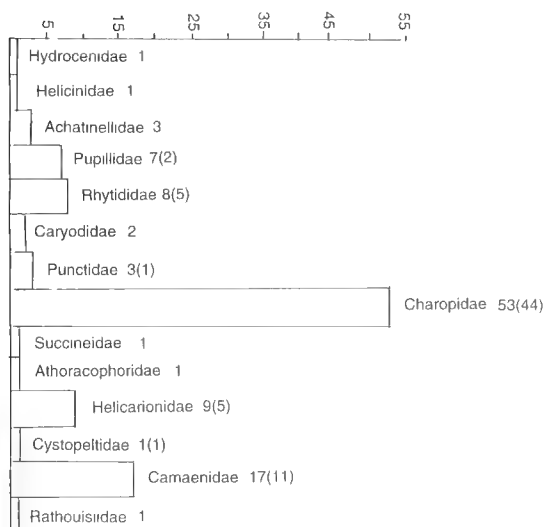


Figure 3. Distribution of Macleay Valley land snails among families. Numbers in brackets indicate undescribed species.

NUMBERS OF SPECIES

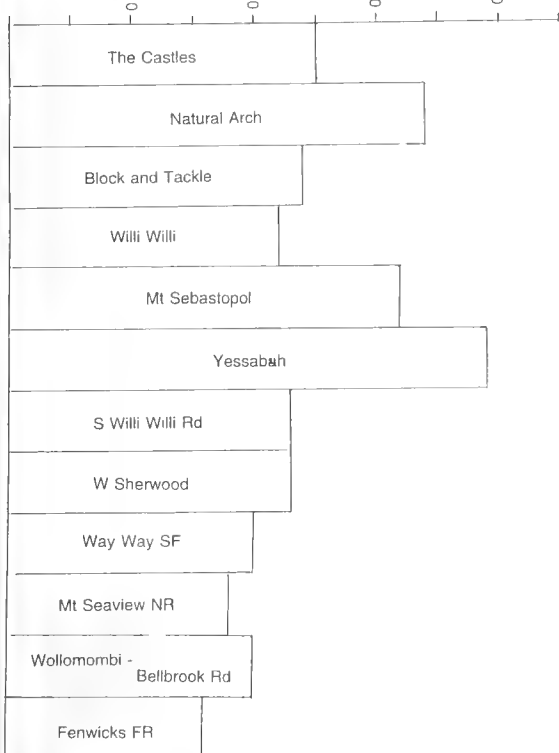


Figure 4. Numbers of species from selected limestone and rainforest sites. First eight localities on left are limestone sites.

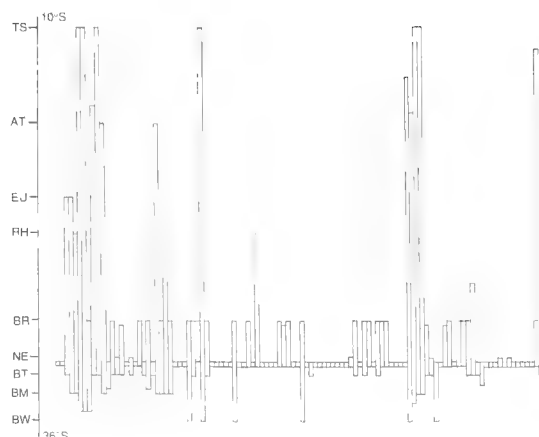


Figure 5. Distribution profiles (north-south) of Macleay Valley land snails along the east coast of Australia. BW = Braidwood; BM = Blue Mountains; BT = Barrington Tops; NE = New England at Armidale; BR = Border Ranges of Queensland/New South Wales; RH = Rockhampton; EU = Eungella west of Mackay; AT = Atherton Tableland; TS = Torres Strait. Study area located between BT and NE. Note the high number of study-area endemics represented by the interrupted line of squares.

Charopidae the endemism is centered on the limestone outcrops and high altitude rainforest areas such as the Carrai Plateau and Fenwicks Flora Reserve. In contrast the camaenid endemics are largely confined to the drier lowland and foothill environments. A significant proportion of species belong to the land snail faunal sub-region which extends from the Border Ranges of southeastern Queensland to Barrington Tops in central New South Wales (Stanisic, 1994: Fig. 2, subfaunal unit G). However, there are also a considerable number of wider ranging species which complement the faunal make-up. The study area is the southern limit for a number of northern subtropical elements including *Papuexul bidwilli* (Reeve, 1853) (Fig. 6B) and the mainly calciphilic Hydrocenidae represented by *Georissa laseroni* (Iredale, 1937) (Fig. 6A).

Within the study area 26 species occurred only within the rainforest biotope including 15 (14 charopids) which are endemic to the study region. Most of these local rainforest endemics (10) were restricted to the warm temperate and cool temperate forests above 800 metres. Of particular note was the subtropical rainforest at Way Way State Forest where 4 endemic species were recorded. Sixteen species occurred only on

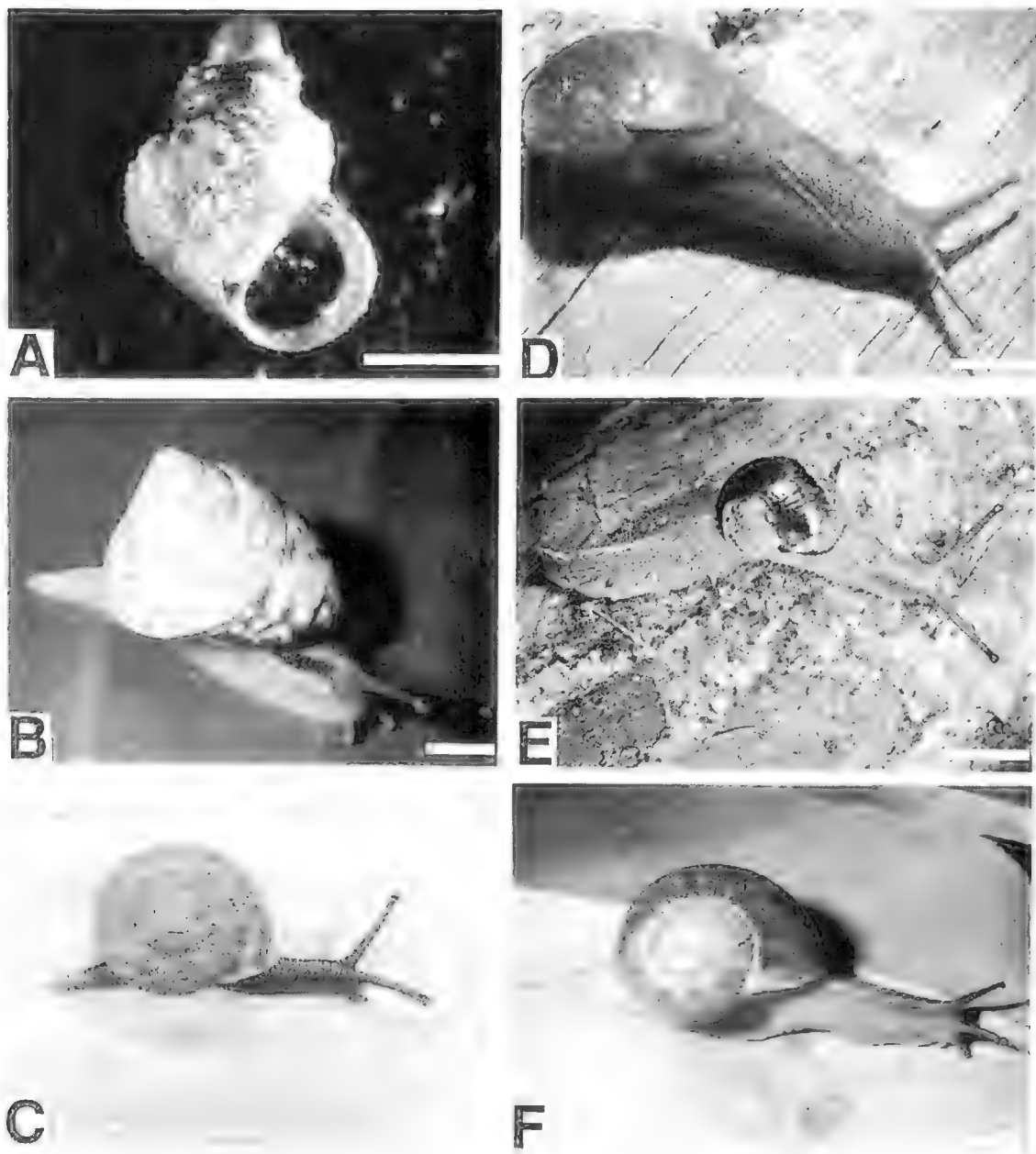


Figure 6. Land snails of the Macleay Valley region. A, *Georissa laseroni*; B, *Papuxul bidwilli*; C, a new species of camaenid from Kippara State Forest; D, *Parmavitrina planilabris*; E, a new semislug from dry habitat near Temagog; F, a new species of carnivorous snail (Rhytididae) from Thumb Creek State Forest. Scale lines: A = 1 mm; B, C = 5 mm; D, E, F = 10 mm.

the limestone outcrops and in no other habitat type. This group of habitat-restricted species included 11 (10 charopids) which are endemic to the region. The more easterly outcrops had the higher levels of endemism. A number of these limestone-restricted species lived on the surface of the karst. These include the charopids *Letomola contortus*, *Coenocharopa yessabahensis* and *Rhophodon kempseyensis* (Stanisic, 1990) as well as *Georissa laseroni*. In absolute contrast the sclerophyllous component of the vegetation mosaic included only 3 species not found in the other habitat types. Not surprisingly the limestone sites showed most affinity with the pure rainforest sites (49 species in common) and very reduced affinity with the sclerophyllous sites (16 species in common).

Discussion

The land snail fauna of the Macleay Valley region in north-eastern NSW is remarkably diverse. Numbers of species per individual site are among the highest in eastern Australia (Stanisic, 1994). The total number of species compares favourably with that of the Wet Tropics biogeographic region (Stanisic et al., 1994). This region (approximately 15–19°S, 145–146°30'E) is considerably larger than the Macleay Valley yet supports only 222 species (185 endemic) on current estimates. In spite of extensive and widespread collecting I do not know of any other area of comparable size in eastern Australia which supports more than 100 species including such a large endemic component.

Land snails are slow moving and particularly prone to desiccation. Both these factors would make them peculiarly sensitive to past events of climatic drying which have reduced rainforests (= closed forests) on the Australian continent to isolated fragments (Adam, 1992). This change to drier conditions has been gradual but presumably involved many episodes of contraction and expansion (Kershaw, 1981) during which time the sclerophyllous forest types came to dominate the landscape. Land snails appear to have retained a high profile in the rainforests with relatively little radiation into surrounding drier forests. This pattern is strongly evident in the Macleay Valley region where 105 (37 endemics) species live in closed forest environments and highlights the importance of rainforest refugia as providers of long term moisture stability. However, the history of environmental change in the Macleay Valley region has been complicated by

the presence of limestone outcrops which have enabled the closed forest habitats to persist in otherwise dry areas. By acting as moisture reservoirs and fire shadows they have provided an important secondary habitat for the land snails. The presence of limestone endemics which exploit the limestone surface as living space and show possible feeding apparatus specialisation (Stanisic, 1990), demonstrates their significance as epicentres of evolution. In sclerophyllous countryside e.g. Yessabah, they provide a stark contrast in species numbers between adjacent habitat types. The Yessabah outcrop supports 39 species yet any surrounding sclerophyll site has less than 10 species. A similar though less remarkable contrast is seen between limestone sites and rainforest sites.

The derivation of this rather unique and diverse regional community of land snails would appear to be intimately tied to the presence of two important snail refugia — limestone and rainforest. In the context of past climatic changes they would have provided 'safe havens' for wider spread species and important centres of evolution as mesic communities were isolated in moist refugia (Galloway and Kemp, 1981). The presence of numerous endemics in the upland rainforests, on limestone karsts, and in isolated refugia such as Way Way State Forest are probable testimony to these past events. Patterns of past connections and subsequent isolation are supported by the presence of disjunctly distributed sister species. The intensity of these historical changes is particularly evident at the dry rainforest-sclerophyll ecotone where a significant radiation of closely related camaenids has occurred. Their distribution patterns suggest a complex history of environmental sifting. In this habitat type, the modern-day influence of annual burning to reduce fuel build-up would also play an important part in the survival of snail populations and species.

Conservation

From a conservation viewpoint the above findings have wide-ranging implications. Limestone habitats are important refugia for land snails. Invertebrates in these habitats often receive indirect protection because of the tourist and recreational potential of limestone caves. However, a large number of outcrops do not contain caves (Lishmund et al., 1986) yet still support significant invertebrate communities, particularly land snails. Some of these species are restricted endemics. From a land snail perspec-

tive all limestones should be included in the National Estate.

There has been a tendency to focus on humid and moist rainforest types in the conservation debate to the detriment of the dry rainforest communities which are widespread in eastern Australia (Gillison, 1987). Their visually unattractive appearance and limited tourist potential has, in some cases, resulted in their large scale and largely uncontested removal e.g. brigalow. Their representation in the National Estate, particularly in north-eastern New South Wales (Floyd, 1987), is poor. This study shows that they are important habitats for land snails and deserve greater consideration in listing proposals.

Finally, it is difficult to see how the outcomes of this study could have been achieved without significant taxonomic input. Much of the invertebrate conservation debate is being reduced to rapid biodiversity assessment which involves limited systematic involvement. Knowledge of species ecology, their degree of endemism and relationships to each other—all essential components of the systematist's craft—have been central to identifying the key conservation issues of this study.

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References

- Adam, P., 1987. *New South Wales rainforests. The nomination for the World Heritage listing*. National Parks and Wildlife Service of New South Wales: Sydney.
- Adam, P., 1992. *Australian rainforests*. Oxford Monographs on Biogeography No.6. Clarendon Press: London.
- Bishop, M.J., 1981. The biogeography and evolution of Australian land snails. Pp.924–954 in: Keast, A. (ed.), *Ecological biogeography of Australia*. W. Junk: The Hague.
- Floyd, A.G., 1980. *Vegetation of Mt Seaview Nature Reserve*. Unpublished report. National Parks and Wildlife Service of New South Wales: Sydney.
- Floyd, A.G., 1983. *Rainforest vegetation of the Yessabah Limestone Belt and Carrai Plateau*. Unpublished report. National Parks and Wildlife Service of New South Wales: Sydney.
- Floyd, A.G., 1987. Status of rainforest in northern New South Wales. Pp.95–117 in: Werren, G. and Kershaw, A.P. (eds), *The rainforest legacy. Australian national rainforests study*. Australian Government Publishing Service: Canberra.
- Galloway, R.W. and Kemp, E.M., 1981. Late Cainozoic environments in Australia. Pp.52–80 in: Keast, A. (ed.), *Ecological biogeography of Australia*. W. Junk: The Hague.
- Gillison, A.N., 1987. The 'dry' rainforest of *Terra Australis*. Pp.305–321 in: Werren, G. and Kershaw, A.P. (eds), *The rainforest legacy. Australian national rainforests study*. Australian Government Publishing: Canberra.
- Kershaw, A.P., 1981. Quaternary vegetation and environments. Pp.81–101 in: Keast, A. (ed.), *Ecological biogeography of Australia*. W. Junk: The Hague.
- Lishmund, S.R., Dawood, A.D. and Langley W.V., 1986. The limestone deposits of New South Wales. *Geological Survey of New South Wales, Mineral Resources* 25; 1–373, +2 maps.
- Nix, H.A., 1981. The environment of *Terra Australis*. Pp.105–133 in: Keast, A. (ed.), *Ecological biogeography of Australia*. W. Junk: The Hague.
- Smith, B.J., 1984. Regional endemism of the south-eastern Australian land mollusc fauna. Pp.178–188 in: Solem, A. and Van Bruggen, A.C. (eds), *World-wide land snails. Biogeographical studies on non-marine Mollusca*. E.J. Brill, Dr W. Backhuys: Leiden.
- Stanisic, J., 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum* 30: 1–241.
- Stanisic, J., 1994. The distribution and patterns of species diversity of land snails in eastern Australia. *Memoirs of the Queensland Museum* 36: 207–214.
- Stanisic, J., Eddie, C., Hill, A. and Potter, D., 1994. *A preliminary report on the distribution of the land snails occurring within the Wet Tropics region*. Unpublished report. Queensland Museum: Brisbane.

THE THREATENED RICHMOND BIRDWING BUTTERFLY (*ORNITHOPTERA RICHMONDIA* [GRAY]): A COMMUNITY CONSERVATION PROJECT

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Abstract

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Destruction of coastal rainforests in south-eastern Queensland and north-eastern New South Wales has led to extinction of *O. richmondia* from two-thirds of its original range and a sharp decline in surviving populations. The species is further threatened by depletion of the butterfly's lowland food plant, *Pararistolochia praevenosa*, and by presence and spread of the Dutchman's Pipe vine, *Aristolochia elegans*, which attracts oviposition but the leaves are toxic to larvae when they attempt to feed. Originally from South America, Dutchman's Pipe has spread from garden cultivation into national parks and reserves. Above 800 m on the Queensland/NSW Border Ranges, *P. laheyana*, also supports birdwing larvae. However, these populations are subject to periodic extinctions, probably due to climatic stress at the higher altitudes where re-colonisation is thought to be dependent on immigrants from lowland populations. Community groups and state national parks authorities are participating in projects to conserve the Richmond birdwing butterfly. The CSIRO's Double Helix Science Club is co-ordinating studies on *P. praevenosa* by students at more than 130 schools, where growth and phenology of 12 vines at each school are being monitored to understand the butterfly's host plant interactions. Aspects of biology of the butterfly and its food plants and strategies which have a bearing on its conservation are discussed.

Introduction

The Richmond birdwing butterfly, *Ornithoptera richmondia* (Gray) has been sometimes treated as a subspecies of the widely distributed, tropical *O. priamus* (Linn.) (Haugum and Low, 1978-1979), or as a distinct species (Zeuner, 1943; D'Abrera, 1975; Common and Waterhouse, 1981) based on its distribution, differences in the male genitalia and sterility of offspring when hybridised with *O. euphorion* (Gray). However, recent reports (A. Hiller, pers. comm.) indicate that these hybrids are not always sterile. Hancock (1983) placed *O. richmondia* in a *priamus* species-group in the genus *Troides* Hubner, subgenus *Ornithoptera*, but subsequently (Hancock, 1991) validated *Ornithoptera* as a separate genus.

Adults of both sexes are similar to *O. euphorion*, although *O. richmondia* is smaller (wingspan of males c. 12-14 cm; females c. 14-16 cm). Adults emerging in spring are often smaller than those emerging in summer and autumn (Common and Waterhouse, 1981), a characteristic attributable to loss of mass in the overwintering pupa. Poor quality of food plants

following drought also leads to reduced size in the developing individuals. In males, the green and the gold spots on the upperside of *O. richmondia* are more restricted than in *O. euphorion* and variable in extent. Haugum and Low (1978-1979) described *richmondia reducta*, with areas of green further reduced, from Grafton and elsewhere. However, this variation is not confined to the southern range of *O. richmondia* indicating that *reducta* is not a valid subspecies. A blue male of *O. richmondia* has been sighted (B. Davies, pers. comm.), a rare colour form also known in *O. euphorion* (R. Magarey, pers. comm.). Blue males which superficially resemble *O. priamus urvillianus* Guérin-Méneville from New Ireland and the Solomon Islands, result from an unusual distribution of the blue and gold scales present in males.

The abundance and distribution of *O. richmondia* have declined since the turn of the century (Illidge, 1927) following destruction of subtropical rainforest supporting *Pararistolochia praevenosa* (F. Muell.) M.J. Parsons (Aristolochiaceae), the principal food plant for its larvae. Originally distributed from Maryborough, south-eastern Queensland to Grafton,

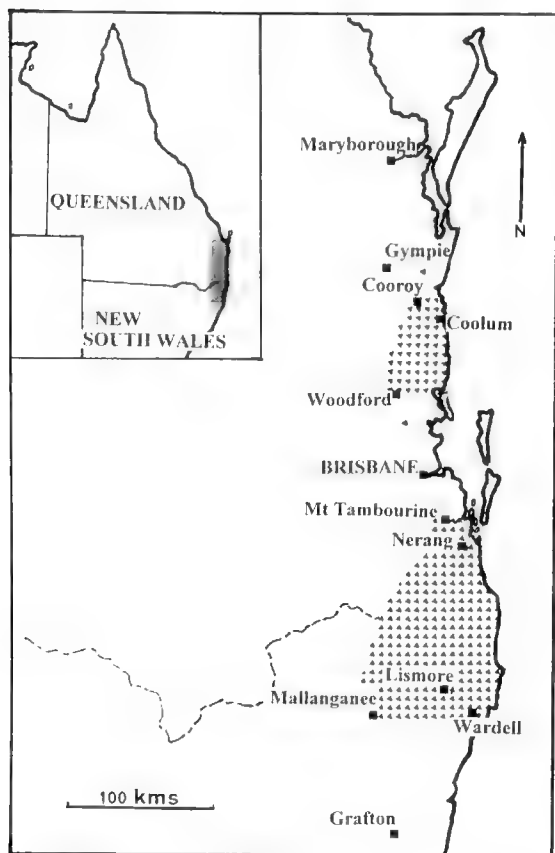


Figure 1. Map showing the distribution (shaded) of *Ornithoptera richmondia* in 1995.

north-eastern New South Wales (Haugum and Low, 1978–1979), the vine and sustained breeding colonies of *O. richmondia* have become extinct from about two thirds of the former northern, central and central parts of its range (Fig. 1). In south-eastern Queensland *O. richmondia* still occurs locally from Yandina to Mt Mee and from Mount Tamborine to the NSW border. An isolated pocket has been observed near Kin Kin. In NSW, the species occurs from Wardell to the Queensland border wherever *P. praeviosa* survives in littoral and lowland rainforest remnants. On the Border and Nightcap Ranges, *O. richmondia* is abundant in the summer months most years where larvae feed on *P. laheyana* (F.M. Bailey) M.J. Parsons. A single female was once sighted near Coffs Harbour (R. Davis, pers. comm.) and one at Toowoomba (J. Macqueen, pers. comm.) in the 1960s but the food plants are not known from these areas.

O. richmondia was last seen near Mary River Heads in 1959 and at Rainbow Beach and Noosa about 1984 (unpubl.). Since the 1920s the but-

terfly has become rare near Brisbane (Illidge, 1927) where the food plants supporting the last breeding colonies were destroyed in the late 1980s. Occasionally ranging adults are seen and larvae have been recently observed on cultivated *P. praeviosa* close to Brisbane and at Mount Glorious (A. Hiller, pers. comm.). The last sightings of *O. richmondia* near Grafton, NSW were made at Susan Island about 45 years ago (J. Seymour/D. Landenberger, pers. comm.). The food plant vines are referred to the genera *Aristolochia* and *Pararistolochia*, following revision of the Australian Aristolochiaceae by Parsons (1996).

Seasonality, biology and ecology

Ornithoptera richmondia is polyvoltine near the coast, adults appearing from late August until May but they are most abundant from September to November and February to April. Near Beewah, Queensland occasional sightings have been made in June and July (A. Powter, pers. comm.). At higher altitudes the species is univoltine with adults mostly appearing from November to February. In favourable years large numbers of adults migrate from the higher altitudes to the lowlands. Such phenomena were observed near Christmas Creek, Queensland in January 1994 and 1995 (M. Houston, pers. comm.) and at Limpinwood, NSW in January 1994 (N. Hepburn, pers. comm.).

The immature stages of *O. richmondia* were described by Common and Waterhouse (1981). The pale yellow eggs (diameter 2.3 mm x 2.0 mm deep, $n = 4$) are deposited usually singly on the underside of mature leaves of the food plant but occasionally on stems or other plants supporting the vines. Occasionally two or more may be deposited on preferred leaves but once 13 eggs were seen on a single leaf of *P. laheyana*. Young foliage utilised by 1st instar larvae is avoided by the ovipositing female. Eggs hatch in 9–13 days. After hatching larvae consume most of their egg-shell and search (up to 2 days) for leaves of appropriate toughness. Instars 1–3 are black or dark purplish-brown with fleshy black spines on all segments except segment 4, which are bright yellow. Fourth and fifth instars may vary from black, brown through to creamish-grey, often with cream fleshy spines on segment 4. There are usually five instars or occasionally six when the nutritional quality of leaves utilised is low. The duration of larval development ranges from 27–46 days ($n = 23$). However, low nutritional quality of the food plant may also protract the rate of development of larvae. During ecdysis, larvae

spin a silken pad beneath a leaf of the food plant or other plant nearby and become torpid for 2–3 days.

Larvae usually leave the food plant to pupate. They select the underside of a leaf (e.g., *Wilkiea* spp., *Ficus coronata* Spin) over which they spin a large silken pad and strengthen the petiole with silk to prevent dislodgment during the protracted pupal phase. Pupae are attached by a cremaster and silken girdle and unlike other species in the genus, are bright green with yellow markings (Common and Waterhouse, 1981) and have an overwintering pupal diapause. In coastal populations most larvae pupating after the last week of January enter diapause and emerge in spring (127–275 days, $n = 8$) while larvae pupating in spring or early summer months emerge within 32–40 days without entering diapause.

Eggs of *O. richmondia* are preyed upon by several species of ants including *Iridomyrmex glaber* (Mayr) and *Pheidole megacephala* (Fab.) an assassin bug (Reduviidae) and the predatory bug, *Oechalia schellenbergia* (Guerin). They are especially susceptible to desiccation during periods of drought. Natural enemies of larvae (mainly instars 1–4) include spiders, the bull ant, *Myrmecia gulosa* (Fab.), the jumper ant, *M. nigrocincta* F. Smith, the soldier beetle, *Chauliognathus atricornis* (Lea) (Cantharidae) and viruses. Cannibalism amongst larvae (mainly instars 1–4) of *O. richmondia* during ecdysis is a major mortality factor. The pupae are occasionally attacked by unidentified hymenopterous parasitoids and when in diapause are subject to desiccation when accompanied by very low temperatures. A pied currawong was observed to peck a pupa but failed to eat it. Adults are sometimes trapped in spiders webs but are rarely attacked by other predators including birds (e.g., noisy pitta).

At high altitudes on the Border Ranges extinctions occur in some years, thought to result from desiccation and extremely low temperatures. These extinctions occur about every 3–7 years after which recolonisation is dependent on immigration from lowland populations.

Food plants of *O. richmondia*

Pararistolochia praevenosa is a locally-distributed vine in lowland, subtropical rainforest (< 600 m) on basaltic slopes, creek banks, or on volcanic alluvial soils bordering rivers and streams. Occasionally *A. praevenosa* occurs in sand dune loams overlying volcanic soils. The

vine may ascend 20 m into the rainforest canopy. Large vines branch close to ground level, producing somewhat flattened mature stems bearing widely-spaced nodes with alternate leaves. On older plants stems sometimes emerge horizontally and layer, developing clumps of vines which climb vertically. Stems may be 1–2 cm in diameter, frequently fusing with other ascending stems. The bark has a distinctive raised, slender reticulated pattern which is easily recognisable at ground level. Vines grow throughout the year particularly after rain, the autumn and winter growth avoiding attack by the larvae of *O. richmondia*. The tough, lanceolate (base slightly cordate) leaf forms with twisted petioles are variable in size, those from alluvial soils tending to have smaller, narrower leaves (c. 16×6 cm) than those from basaltic soils (> c. 22×10 cm). The flowers (September–November) are pollinated by midges (*Forcipomyia* spp.; Ceratopogonidae; G. Monteith, pers. comm.). The orange fruit when ripe (March–April) fall intact to the ground where they are dispersed by ground birds, particularly brush turkeys. Seeds are macerated and some buried by the feeding birds which results in the germination of clusters of seedlings.

Understorey vertical growth of *P. praevenosa* bearing young leaves is selected by ovipositing females and preferred by larvae while tall canopy growth is less frequently utilised. However, the quality of soft foliage of *P. praevenosa* acceptable to newly-eclosed larvae is limited since they exclusively require young, soft leaves near the apex of an actively growing vine. Even young leaves at the 6–8th node from the apex may be too tough to support feeding. While late 2nd and later instars will consume the firmer leaves, flowers, seeds and softer stems, 1st instar larvae survive only on sub-apical, expanding leaves and avoid the pubescent growing tip. On *P. praevenosa* when soft foliage is limited, larvae of *O. richmondia* prey on others undergoing ecdysis. Rarely will more than two larvae share leaves on the same stem without attacking one another. The pupae are also susceptible to cannibalism when larvae are deprived of sufficient soft foliage.

Experiments were carried out to determine the toughness of leaves of *P. praevenosa*, acceptable to newly-eclosed larvae of *O. richmondia*. Larvae were held in organza sleeves with leaves attached to plants, selected with progressively increasing toughness using a leaf penetrometer described by Sands and Brancatini (1991). These experiments showed that leaves exceed-

ing a toughness (force) of 0.23 newtons/mm² were too tough for first instar larvae and they starved without feeding. Thus, leaf toughness of *P. praevenosa* appears to contribute significantly to survival and abundance of *O. richmondia*. Leaf toughness of *P. praevenosa* was estimated to account for 85% of starvation by first instar larvae (n=183) between 1986 and 1988 at a breeding site.

In montane rainforest above 800 m, on the NSW, Queensland Border Ranges, larvae of *O. richmondia* feed on *P. laheyana*. This plant occurs as an understorey vine on basaltic ridge tops and occasionally slopes where it is much less robust than *P. praevenosa*. *P. laheyana* is a horizontal, as well as vertical climber rarely ascending more than 4 m. The smooth and slender stems (c. < 0.8 cm) frequently branch and bear small (c. 12 x 4 cm) leaves which are softer than *P. praevenosa* and most young growth is acceptable to first instar larvae. As larvae mature, leaves and the softer stems of *P. laheyana* may be consumed. Sometimes plants may be rendered leafless by gregarious larvae but they rapidly respond with growth when larvae are not present. Thus the equivalent biomass of *P. laheyana* has a greater carrying capacity for larvae than *P. praevenosa*, a factor believed to explain the greater abundance often observed at higher altitudes.

The larvae of *O. richmondia* will develop when fed from eclosion, on *Aristolochia tagala* Chamisso, a food plant for *O. euphorion* and several other birdwing butterflies Jebb (1993). However, eggs deposited on young leaves of this vine frequently fail to eclose. At the site of contact on a leaf, a raised necrotic patch of tissue develops, indicating a reaction by the plant to the egg or its accompanying secretions.

Adult *O. richmondia* visit the flowers on many different plants to gather nectar, preferring white and red blooms. *Ornithoptera* spp. and *Delias* spp. (Pieridae), comprise two of the few butterfly genera that visit flowers of red bottlebrush (*Callistemon* spp.). Native flowers favoured include *Syzygium* spp., *Eucalyptus* spp., *Lophostemon confertus* (R. Br.) Wilson and Waterhouse, *Flagellaria indica* L., *Melicope elle-ryana* (F. Muell.) T. Hartley, *Alloxylon pinnata* (Maiden and Betche) and *Grevillea* spp. as well as many exotic species.

Conservation program

Many fragile breeding habitats for *O. richmondia* continue to be destroyed despite community

conservation efforts. At Coolum, the northern coastal limit on the Sunshine Coast, a breeding site was recently threatened by home unit development while another colony on the Nerang River may now be safe after intensive lobbying by a local conservation group. Pressures on populations from collectors of adult *O. richmondia* are negligible, provided that many immature stages are not removed from breeding sites. Bushfires destroyed several sites during November 1994 in an exceptionally dry season.

The ornamental Dutchman's Pipe vine, *Aristolochia elegans* Mast., originally from South America, attracts oviposition by *O. richmondia* but it is poisonous to the early instar larvae when they attempt to feed on its leaves (Straatman, 1962). This vine has escaped cultivation to become a weed in forestry reserves, national parks and many of the riverine habitats previously occupied by *P. praevenosa*. Egg counts made on both *A. elegans* and *P. praevenosa* in Burleigh Heads National Park showed a marked preference for the exotic species by the ovipositing butterflies. Between 1981 and 1992 counts showed that eight times more eggs (n = 486) were deposited on *A. elegans* than on *P. praevenosa*. Most larvae attempting to feed on *A. elegans* died in the first instar but a few reached third instar. Fortunately the Dutchman's Pipe vine is easily eradicated. Over the last two summers an officer working in Burleigh Heads National Park has successfully controlled the vine, encouraging other authorities and community groups to undertake similar eradication programs. Widespread media publicity against growing and selling the vine has generally led to its removal from suburban gardens.

The conservation status of the Richmond birdwing is considered 'vulnerable' (IUCN category), although not previously classified by Collins and Morris (1985). A conservation strategy for the butterfly is underway based on cultivation of *P. praevenosa* in gardens, environmental reserves and schools. The project began in 1992, sponsored by the NSW National Parks and Wildlife Service. Balunyah Nursery at Coraki, NSW were provided with seedlings, cuttings and seeds of *P. praevenosa* enabling them to develop stocks of for distribution to other nurseries. To date more than 15 000 vines have been distributed to retailers and community groups participating in the program. Community participation expanded rapidly and in 1993 CSIRO's Science Education Program, the Double Helix Club was approached to co-ordinate the projects. By combining the scientific

and education expertise of officers from both Organisations, students began to participate in research and the conservation program.

The success of the program is reflected by the magnitude of community involvement. More than 130 schools between Grafton and Maryborough are currently involved in the project. Each school has planted 12 vines which will supplement the diminishing wild food plants and provide breeding corridors for areas without vines. Temperatures, rainfall and growth parameters of the vines are being measured as part of the coordinated Double Helix Club program. Schools will be evaluating a new leaf penetrometer, conducting experiments on the vines, and collecting and identifying insect pollinators from the flowers of *Pararistolochia* spp.. They assist with locating Dutchman's Pipe in bushland and provide community awareness and advice for removal of the vine from cultivation when it threatens the progeny of ovipositing *O. richmondia*. As well as educating for conservation, they are encouraging cultivation of *P. praevenosa* and have developed a strong sense of ownership towards protecting the butterfly.

Dispersing female *O. richmondia* have oviposited on cultivated vines at Alstonville, near Brisbane and at Beerwah, where urban environments do not appear to inhibit re-establishment of the butterflies. Queensland's first butterfly habitat reserve for the Richmond birdwing was designated at the Stanley River Rehabilitation Project, by the Queensland Department of Primary Industry and a Land Care group. The South Bank Corporation in the heart of Brisbane, has nominated 'Butterfly Island' for student and public education and planted the island with 30 *P. praevenosa*.

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References

- Collins, N.M. and Morris, M.G., 1985. *Threatened swallowtail butterflies of the world*. The IUCN red data book. IUCN Gland, Switzerland.
- Common, I.F.B. and Waterhouse, D.F., 1981. *Butterflies of Australia*. Angus and Robertson: Sydney.
- D'Abrera, B., 1975. *Birdwing butterflies of the World*. Lansdowne Press: Melbourne.
- Hancock, D.L., 1983. Classification of the Papilionidae (Lepidoptera): a phylogenetic approach. *Smithersia* 2: 1-48 [National Museums and Monuments of Zimbabwe].
- Hancock, D.L., 1991. Notes on the phylogeny and biogeography of Ornithoptera Boisduval (Lepidoptera: Papilionidae). *Tyo to Ga* 42: 17-36.
- Haugum, J. and Low, A.M., 1978-1979. *A monograph of the birdwing butterflies*. Vol. 1 (2). Scandinavian Science Press: Klampenborg.
- Illidge, R., 1927. Brisbane butterflies of the family Papilionidae. Series II. *Queensland Naturalist* 6: 33-39.
- Jebb, M., 1993. *Aristolochia in New Guinea*. Unpublished guide, Christensen Research Institute: Madang, Papua New Guinea. 51 pp.
- Parsons, M.J., 1996. New species of *Aristolochia* and *Pararistolochia* (Aristolochiaceae) from Australia and New Guinea. *Botanical Journal of the Linnean Society*, 120: 199-238.
- Sands, D.P.A. and Brancatini, V.A., 1991. A portable penetrometer for measuring leaf toughness in insect herbivory studies. *Proceedings of the Entomological Society of Washington* 93: 786-788.
- Straatman, R., 1962. Notes on certain Lepidoptera ovipositing on plants which are toxic to their larvae. *Journal of the Lepidopterists Society* 16: 99-103.
- Zeuner, F.E., 1943. Studies on the systematics of *Troides* Hubner (Lepidoptera Papilionidae) and its allies; distribution and phylogeny in relation to the geological history of the Australasian archipelago. *Transactions of the Zoological Society of London* 25: 107-184.

SPECIES RICHNESS AND ENDEMISM OF BAEINE WASPS (HYMENOPTERA: SCELIONIDAE) IN AUSTRALIA

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Abstract

Iqbal, M. and Austin, A.D., 1997. Species richness and endemism of baeine wasps (Hymenoptera: Scelionidae) in Australia. *Memoirs of the Museum of Victoria* 56(2): 455-459.

The species richness and level of endemism of baeine scelionid wasps, which are endoparasitic on spider eggs, were determined for four sites of urban bushland in the Perth area and among four more distant localities across the Australian continent. Among the Perth sites the number of baeine species varied from 14 to 20, with a total number of 27 for the sites combined. The proportion of species shared among sites was high, 55-71%, but 22% of species were only recorded at one site. The four distant locations which had different vegetation types, viz. Western Australia (Perth), South Australia (Mt Barker), and north and south-east Queensland (Split Rock and Mt Glorious), varied in number of species from 20 to 31 (total of 97 species) but with virtually no species in common among them. These results are discussed in relation to differences in habitat preference, collecting techniques, the size of the Australian baeine fauna, and a possible trophic level relationship between spider and baeine species richness (i.e. host and parasitoid).

Introduction

In recent years comprehensive surveys of invertebrates using multiple trapping techniques have shown that the insect order Hymenoptera to be one of, if not the most, species rich ordinal taxa of animals (LaSalle and Gauld, 1992, 1993). This is particularly obvious from surveys in tropical forests (Askew, 1990; Naumann et al., 1991; Noyes, 1989a, 1989b) but generally it applies across most terrestrial habitats (LaSalle and Gauld, 1993). Like the other huge orders of insects, the Hymenoptera comprise a large number of functional groups, including herbivores (exposed leaf-feeders, leaf miners, gall formers, seed feeders, pollen and nectar feeders, and xylophagous species), predators, parasitoids (both ecto- and endoparasitoids), and hyperparasitoids (see Gauld and Bolton, 1988). However, it is one functional group, the parasitoids, that is responsible for the species richness of the order. Parasitoids exploit arthropods as a food source for their developing larvae and they have radiated into this almost unlimited resource, producing a phenomenal number of species, probably several hundred thousand world-wide. It is this biology, associated with their high degree of host specificity, that has lent them to being utilised as biological control agents of insects.

One group of small scelionid parasitoids, the Baecini (< 2 mm in length), endoparasitically attack the eggs of spiders (Austin, 1985), and

they are postulated to be important regulating agents of spider populations (Austin, 1984a). Given that spiders are becoming one of the preferred groups as ecological indicators, to assess such aspects as general species richness, habitat disturbance, faunal community structure and biogeographic relationships (see Churchill, 1997; Harvey et al., 1997; Main, 1997; York, 1997), a comparable knowledge of the distribution patterns, richness and levels of endemism of baeine wasps may allow such ecological questions to be examined and compared between trophic levels, i.e. between spiders and their parasitoids. In this respect, the current study documents distribution patterns and composition among baeine wasps for a number of sites within the Perth urban area, and among four distant localities across the Australian continent which vary substantially in habitat type.

Methods

Four sites around the Perth urban area were selected to assess baeine species richness, and they represented areas of remnant native vegetation which were used in a more extensive study by Harvey et al. (1997). These were located at Bold Park, Perth Airport, Tuart Hill and the Talbot Road Reserve, and they generally comprise open *Eucalyptus-Banksia* woodland. The collecting method at these sites was three or

four grids, each of 10 2-l plastic ice-cream containers charged with concentrated (95%) ethylene glycol and run for 12 months. It was not possible to use other collecting techniques around Perth, such as Malaise traps, because of the high risk of vandalism (see Harvey et al., 1997 for more detailed description of the sites and collecting method). Specimens were removed from traps about every six weeks; they were then washed, transferred to 70% ethanol and sorted under a stereomicroscope, point-mounted and labelled.

Taxonomically, baeine scelionids are well-known at the generic level (Galloway and Austin, 1984). Further, sufficient information is available at the species level to accurately separate morphospecies (e.g. Austin, 1981, 1984b, 1986, 1995), even though the majority are undescribed. Characters found to be particularly important in separating species include the relative size and shape of body segments and tergites, surface sculpturing, length and shape of antennal segments, presence and size of a metasomal horn, development of wings, length of veins, wing pilosity, and colour pattern.

To assess regional (continent wide) levels of baeine richness and endemism, the data from the four Perth sites were pooled and compared with that from three additional localities. These data were collected in an *a posteriori* fashion, i.e. they were accessed from existing material in museum collections (primarily the Australian National Insect Collection, Canberra and Department of Primary Industries, Brisbane). These sites were selected because they have been extensively collected, they are very distant from each other, and they represent very different habitat types. They are Mt Barker summit, 30 km ESE of Adelaide, SA, comprising disturbed open mallee woodland; Mt Glorious summit, a well-known rainforest site in SE Queensland; and Split Rock, north Queensland, comprising tropical savannah. The collecting methods and duration of trapping varied among the four locations as indicated in Table 2. However, the techniques employed were chosen to optimise the wasp catch at each location. A Malaise trap was used at Mt Barker, Mt Glorious and Split Rock, a flight-intercept trap (FIT) was deployed at the latter two locations, while sweep-netting was only undertaken at Mt Glorious (N.B. the latter technique did not yield any additional species). Further, the six month duration of trapping at Mt Barker is probably equivalent to the 12 months at the other locations, given that previous experience has shown that

baeine wasps are hardly ever collected there during the winter months and, when specimens have been taken, they have represented common summer-active species. As for the pitfall traps at Perth, the FIT at Split Rock used ethylene glycol as a preservative, while the Malaise traps used 70% ethanol.

Results and discussion

The genera and number of baeine species for the four sites around Perth are given in Table 1. The number of genera varied little, from five to six, but the composition was different among sites, with no site having all seven genera. The number of species varied from 14 at Tuart Hill to 20 at Bold Park, with a total of 27 species recorded across all sites. Of these, 14 species (52%) are either wingless or micropterous, including all females of *Baeus* Haliday, *Mirobaeoides* Dodd and *Mirobaeus* Dodd, and three species of *Idris* Foerster (data not shown), while the majority of *Idris* and *Ceratobaeus* Ashmead, and all *Odontacolus* Kieffer and *Hickmanella* Austin are fully winged. The overlap in species composition among sites is shown in Figure 1. It varied from 55% (Bold Park versus Tuart Hill) to 71% (Tuart Hill versus Talbot Road and Perth Airport), although six species (22%) were restricted to just one site. However, more extensive collecting at the four sites is likely to increase the number of shared species.

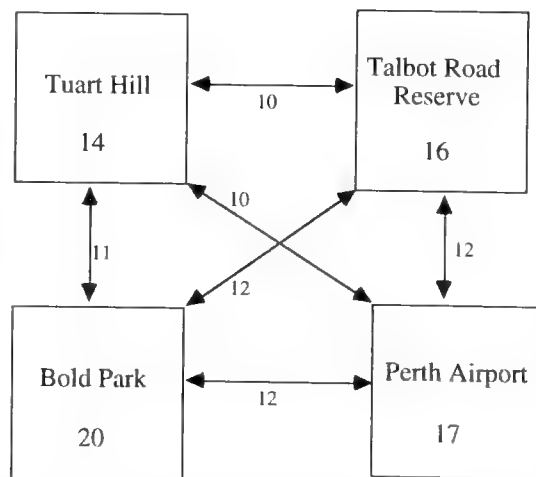


Figure 1. Number of baeine scelionid species shared between the four sites of remnant vegetation in the Perth area.

Table 1: Number of species of baeine scelionid wasps at four sites in the Perth urban area.

Genus	Sites			
	Tuart Hill	Talbot Rd Reserve	Bold Park	Perth Airport
<i>Baeus</i>	2	2	2	2
<i>Ceratobaeus</i>	—	2	3	3
<i>Hickmanella</i>	1	1	1	—
<i>Idris</i>	4	5	7	4
<i>Mirobaeoides</i>	6	6	6	5
<i>Mirobaeus</i>	1	—	—	1
<i>Odontacolus</i>	—	—	1	2
Total	14	16	20	17

Table 2: Number of species of baeine scelionid wasps at four localities in Australia

Locality	Perth, WA	Mt Barker, SA	Mt Glorious, SE Qld	Split Rock, N Qld
Trap type	Pitfall	Maliase	Maliase, FIT, Sweeping	Maliase, FIT
Duration	12 months	6 months	Sporadic, long term	12 months
<i>Baeus</i>	2	1	2	—
<i>Ceratobaeus</i>	4	11	15	10
<i>Hickmanella</i>	2	—	—	—
<i>Idris</i>	8	8	12	11
<i>Mirobaeoides</i>	8	—	1	1
<i>Mirobaeus</i>	1	—	—	—
<i>Odontacolus</i>	2	—	1	1
Total	27	20	31	23

Data for the four Perth sites was pooled and is presented along with the three distant localities, Mt Barker, Mt Glorious and Split Rock in Table 2. Because of differences in collecting techniques, number of traps, and duration of sampling the data are only generally comparable. However, they are most similar for the three eastern localities, all of which approximate 12 months collecting and used similar traps.

The number of genera varied more significantly than among the four Perth sites, from seven at Perth (combined) to three at Mt Barker, while the number of species varied from 20 at Mt Barker to 31 at Mt Glorious (Table 2), with a total of 97 species. Further, the species composition varied substantially among Perth and the other three localities in the number of apte-

rous/micropterous forms, from 4–5% (one species) at Mt Barker and Split Rock to 26% (eight species) at Mt Glorious and 52% at Perth (see above). These differences are primarily reflected in the numbers of *Mirobaeoides* spp., all of which have apterous females. Whereas the four sites at Perth had eight species, the other three locations had one or none. The richness of this genus around Perth is particularly surprising, given that a recent revision of *Mirobaeoides* for the whole continent (Austin 1986) recorded only 12 species, most of which are apparently restricted to the eastern seaboard. Like Perth, the other three localities were dominated by *Ceratobaeus* and *Idris* spp. but even more so, i.e. 87% or more of the total species. The reasons for the above differences among locations are not

clear. They could be arifactual and the result of different collecting techniques, or they could reflect real differences in habitat preferences and levels of endemicity among genera and species. Quite probably, both factors are involved. As might be expected, the locality with the highest proportion of apterous/micropterous species (Perth) was the one where only pitfall traps were used, a technique that is likely to optimise the catch of ground-inhabiting, reduced-winged forms. However, flight interception traps also catch ground-living species (Austin pers. observ.) and in the two locations, Mt Glorious and Split Rock, where these traps were employed, the proportion of apterous/micropterous forms was surprisingly much lower.

Where the number of species shared among the Perth sites exceeded 50%, that among the four distant locations was very low. Only two species were shared between Perth and Mt Barker, and a further two between Perth and Mt Glorious (i.e. 7%), while no species were shared among Mt Barker, Mt Glorious and Split Rock.

Although the species recorded at the four localities undoubtedly occur more widely, the fact that there is very little overlap in the fauna among localities indicates that many baeines have restricted distributions, e.g. no species in common between the eastern sites (Mt Glorious and Split Rock). These data raise the question — what is the true size of the Australian baeine fauna? Recent surveys by us, based on examination of Australian and overseas collections, and extensive field work over the last 15 years by one of us (ADA) show that the number of described species conservatively represents only about one-sixth of the estimated total number (Table 3). Already, about 150 species each of *Idris* and *Ceratobaeus* have been recognised. This estimate is based on the number of species identified in collections, increased by a factor of approximately 20–25% to account for as yet unrecorded new species. Indeed, new species have been collected within the last 12 months from relatively well-collected habitats close to major Australian cities. Further, the level of endemism indicated in this study among geographically close and distant localities strongly suggest that areas of the continent that have not been collected or only poorly surveyed (for which there are many) are likely to yield many new species. Therefore, our estimated increase of 20–25% over and above the currently known species, may be far too conservative.

Table 3. Recorded and estimated number of Australian baeine species

Genus	Described species	Estimated species
<i>Baeus</i>	3	20
<i>Ceratobaeus</i>	31	200
<i>Hickmanella</i>	4	10
<i>Idris</i>	27	200
<i>Mirobaeoides</i>	15	35
<i>Mirobaeus</i>	2	15
<i>Odontacolus</i>	3	20
Total	85	500

Whether or not the species richness of baeine wasps is related to that of their host spiders is yet to be determined. However, the present study provides the background and means for this to be undertaken, at least at the four urban bushland sites around Perth (see Harvey et al., 1996). If baeine richness is so related, then these small wasps may prove an important adjunct to studies on the diversity of spiders, and to examining species richness between trophically linked groups, viz. invertebrate hosts and their insect parasitoids. One aspect of the biology of baeine wasps that is yet to be investigated and which is likely to impinge on both of these questions (the size of the continent's fauna and whether baeine and host species richness are linked) is their level of host specificity. Preliminary studies on four species of baeines indicate that they are specific to at least a single spider genus, and possibly more narrowly to a species-group (Austin, 1984a). If this is the case, then the total number of baeine species will be dictated, to a large degree, by the number of genera/species-groups they have evolved to exploit. Clearly, not all spiders are attacked by baeine wasps. For instance, they are not recorded from mygalomorph eggs, whereas they are known from many araneomorph species (Austin, 1985). However, for the great majority of araneomorphs such information is just not available.

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References

- Askew, R.R., 1990. Species diversities of Hymenoptera taxa in Sulawesi. Pp. 255–260 in: Knight, W.J. and Holloway, J.D. (eds), *Insects and the rainforests of south-east Asia (Wallacea)*. The Royal Entomological Society: London. 343 pp.
- Austin, A.D., 1981. *Hickmanella*, a new genus of Scelionidae from Australia (Hymenoptera: Proctotrupoidea). *Journal of the Australian Entomological Society* 20: 303–308.
- Austin, A.D., 1984a. The fecundity, development and host relationship of *Ceratobaeus* spp. (Hymenoptera: Scelionidae), parasites of spider eggs. *Ecological Entomology* 9: 125–138.
- Austin, A.D., 1984b. Species of *Ceratobaeus* Ashmead (Hymenoptera: Scelionidae) from south-eastern Australia. *Transactions of the Royal Society of South Australia* 108: 21–34.
- Austin, A.D., 1985. The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. *Journal of Natural History* 19: 359–376.
- Austin, A.D., 1986. A taxonomic revision of the genus *Mirobaeoides* Dodd (Hymenoptera: Scelionidae). *Australian Journal of Zoology* 34: 315–337.
- Austin, A.D., 1995. New species of scelionid wasps (Hymenoptera: Scelionidae: Baecini) from Western Australia, parasitic on spider eggs. *Records of the Western Australian Museum Supplement* 52: 253–263.
- Churchill, T.B., 1997. Spiders as indicator taxa: an overview for Australia. *Memoirs of the Museum of Victoria* 56: 331–337.
- Galloway, I.D. and Austin, A.D., 1984. Revision of the Scelioninae (Hymenoptera: Scelionidae) in Australia. *Australian Journal of Zoology Supplementary Series* No. 99: 1–138.
- Gauld, I. and Bolton, B., 1988. *The Hymenoptera*. British Museum (Natural History), London and Oxford University Press: Oxford, 332 pp.
- Harvey, M.S., Waldo, J.M., How, R.A. Dell, J., and Kostas, E. 1997. Biodiversity and biogeographic relationships of selected invertebrates from urban bushland remnants, Perth, Western Australia. *Memoirs of the Museum of Victoria* 56: 275–280.
- LaSalle, J. and Gauld, I.D., 1992. Parasitic Hymenoptera and the biodiversity crisis. (4th European Workshop on Insect Parasitoids). *Redia* 64: 315–334.
- LaSalle, J. and Gauld, I.D., (eds) 1993. *Hymenoptera and biodiversity*. CAB International: Wallingford. 348 pp.
- Main, B.Y., 1997. Tropical rainforest spiders in the Australian desert: the irony of an adaptive legacy. *Memoirs of the Museum of Victoria* 56: 339–347.
- Naumann, I.D., Weir, T.A. and Edwards, E.D., 1991. Insects of Kimbley rainforests. Pp. 299–332 in: McKenzie, N.L., Johnston, R.B. and Kendrick, P.G. (eds), *Kimbley rainforests*. Surrey Betty and Sons: Chipping Norton. 490 pp.
- Noyes, J.S., 1989a., The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecological Entomology* 14: 197–207.
- Noyes, J.S., 1989b. A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History* 23: 285–298.
- York, A., 1996. Assessing ecological sustainability and biodiversity conservation — the use of performance indicators in forest management. *Memoirs of the Museum of Victoria* 56(2).

HIDDEN BIODIVERSITY: DETECTION OF CRYPTIC THYNNINE WASP SPECIES
USING SEXUALLY DECEPTIVE, FEMALE-MIMICKING ORCHIDS

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Abstract

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Cryptic or sibling species are difficult to detect by external morphological characters alone, and represent hidden biodiversity. One group in which such species commonly occur is the large and predominantly Australian flower wasp subfamily Thynninae (Hymenoptera: Tiphiidae). Many thynnine species are pollinators of sexually deceptive orchids in the subtribe Caladeniinae. For example, male wasps of the genus *Neozeleboria* Rohwer are attracted by pseudophoromones produced by flowers of the genus *Chiloglottis* R. Br. Pollination occurs when males attempt to copulate with structures on the orchid labellum that mimic the wingless, ant-like female. Such wasp-orchid relationships may be species specific within their normal environmental range, and can be used to supplement classical alpha taxonomy. Field baiting experiments (using picked flowers to attract wasps) have provided large numbers of wasp specimens and evidence of numerous unexpected cryptic species. An example is discussed involving three closely related orchids, *Chiloglottis trilabra* Fitzg., *C. reflexa* Labill and *C. seminuda*, D.L. Jones and their respective pollinators, *Neozeleboria proxima* (Turner) and two new cryptic species of *Neozeleboria*.

Introduction

Cryptic or sibling species are notoriously difficult to detect (Paterson, 1990) and represent hidden biodiversity. By definition cryptic species cannot be separated easily by traditional alpha taxonomic methods. They are usually revealed by the presence of biological discontinuities (Paterson, 1990), such that some populations behave differently to others thought to be the same species. This is often interpreted as intraspecific variability, when in fact a complex of sibling species may be present. When biological discontinuities in complexes of sibling species are recognised, close examination of the morphology will often, but not always, reveal discrete, consistent differences amenable to circumscription by alpha taxonomic methods (Drew and Hardy, 1981; Whittle et al., 1987). Unequivocal proof of the existence of sibling species requires evidence of genetic or reproductive isolation in sympatric populations (Mahon et al., 1982).

In this paper we report on studies which have led to the recognition of cryptic species in thynnine (Tiphiidae: Thynninae) wasps that pollinate sexually deceptive orchids. The subtribe Caladeniinae of the Orchidaceae contains several genera with species exclusively pollinated by male thynnine wasps (Stoutamire, 1974,

1975, 1983). The males are attracted to the orchids by odours that appear to mimic the sex pheromones of the female. Flowers are then pollinated when the males attempt to mate with the orchid labellum, which mimics the shape and/or colour of the female.

Various studies have suggested that a specific relationship exists between each orchid species and a single thynnine species (Stoutamire, 1983, 1986; Peakall, 1990; Handel and Peakall, 1993; Peakall and Handel, 1993). However, recent studies (Bower, 1992, 1996) have shown that sexually deceptive species of Caladeniinae may attract more than one thynnine visitor, but only one, or occasionally two, of these is capable of effecting pollination.

One of us (CCB) has been using this specific relationship to identify cryptic species of orchids (Bower, 1992, 1996). Samples of flowers from two or more orchid populations thought to represent different taxa are exposed simultaneously in the field in pollinator choice tests. If orchid samples consistently attract different thynnine species they are reproductively isolated and represent different species (Paulus and Gack, 1990). Several new cryptic species of orchids in the genus *Chiloglottis* R. Br. have been detected by these methods (Bower, 1996). In the course of this work it became apparent

there were also cryptic species of thynnines among the pollinators of *Chiloglottis*.

This paper presents the methodology we have used to demonstrate the existence of cryptic thynnine species. An example is presented of the use of pollinator choice tests in the field to detect two undescribed sibling wasp species among the pollinators of a group of three cryptic orchid species in the *Chiloglottis reflexa* (Labill) Druce group.

Methods

Orchids studied

Chiloglottis are small terrestrial herbs that occur in sheltered locations in open forests on the coast and ranges of eastern Australia. Plants consist of a small underground tuber, twin lanceolate, prostrate leaves and a single small flower on a slender stem about 5–12 cm high. The labella of *Chiloglottis reflexa* group species are about 10 mm long and have prominent clusters of dark, glandular calli which collectively mimic the ant-like female of the thynnine wasp pollinator. Males are attracted to the flower and attempt to mate with this pseudofemale. In so doing the dorsal thorax of the male contacts the overhanging anther and removes the pollinia which are subsequently wholly or partially transferred to the stigmas of other flowers he may visit.

Three similar, sympatric, autumn flowering species in the *Chiloglottis reflexa* group from the Blue Mountains region of the NSW central tablelands and the Wollongong area on the south coast were studied. *Chiloglottis reflexa* and *C. seminuda* D. Jones frequently occur together on sandy soils, while *C. trilabra* Fitzg. prefers heavier soils at high altitudes and may overlap on shales with *C. seminuda*. In areas with complex geology all three species may occur in close proximity, e.g., at Mt Wilson where basalt overlies sandstone. *Chiloglottis reflexa* and *C. trilabra* are difficult to separate taxonomically (Jones, 1988). Samples of *C. trilabra* from the northern (Serpentine Nature Reserve) and southern (Batlow) tablelands were used in some tests.

Pollinators of *Chiloglottis*

Chiloglottis species are pollinated by small thynnine wasps of the genus *Neozeleboria* (Stoutamire, 1975; Bower, 1992, 1996; Handel and Peakall, 1993; Peakall and Handel, 1993), and two recently recognised undescribed genera (Brown, unpublished). The *Chiloglottis reflexa* group is pollinated by *Neozeleboria proxima* and its allies, the males of which are 8–13 mm long,

and black with orange legs and yellow markings on the head and body.

Field techniques

Chiloglottis flowers were exposed in the field with their stems in small glass vials (13 × 50 mm) of water mounted in a wood block placed on the ground in suitable habitat. Three flowers from the same population of each taxon were placed in each vial. Up to 5 sets of flowers placed in a line 35–40 cm apart could be monitored simultaneously in choice experiments. As far as possible the line of vials was oriented perpendicular to the wind direction to minimise overlap of the pheromone trails close to the blocks.

Flowers were exposed for a standard 3 min at each site since most males arrived within the first few minutes of an exposure (Peakall, 1990). By moving flowers to a new site 20 m or more away, a renewed response could be obtained by sampling a new segment of the wasp population. The number of exposure sites used at each locality depended on wasp abundance. New exposure sites were selected until a sample of 20 or more wasps was obtained for each orchid taxon eliciting a response. For scarce or patchily distributed wasps it was not always possible to obtain samples of this size.

Insects were only considered to be attracted to a set of flowers if they:

1. landed on or within 5 cm of the flowers;
2. approached flowers directly in flight to within about 10 cm; and/or
3. circled flowers closely in flight.

Thynnine wasps or other insects which made general approaches to the area, and did not clearly single out flowers were ignored. Wasps meeting the above criteria were captured by rapidly lowering an insect net over them and the flowers, with the mesh held clear of the flowers to prevent damage.

Experimental design

Three designs of field tests have been used to establish the preferences among thynnine pollinators for specific orchid taxa (Bower, 1996).

1. **Sympatric choice test:** Two or more sets of flowers of different or suspected different taxa from the same geographic region are exposed together.
2. **Allopatric choice test:** Samples of closely related orchid taxa from different geographic regions are exposed together in each of their regions and habitats.
3. **Sequential test:** This tests for variation in attractiveness to wasps of different sets of flowers of the same species. It aims to deter-

mine whether nil responses to flowers in previous choice tests were due to the greater attractiveness of other conspecific sets of flowers. It consists of two parts: (a) a 3 min exposure of sets of flowers with low or nil responses in a previous choice test, followed at the same site by (b) a further 3 min in which previously attractive flowers are added to the array as controls.

Responses by wasps in the first 3 min to previously unattractive flowers show they have similar pseudophoromones and may be the same species as the more attractive samples. If the flowers remain unattractive and there is a response to the control, they are different taxa.

The above tests enable cryptic orchid species to be distinguished, provided the pollinators are readily separable (Bower, 1996). However, if the pollinators also belong to a complex of cryptic taxa, further tests are needed to isolate both the orchid and wasp species. This is done by conducting choice tests with the same orchid samples at a number of localities in appropriate habitats. By chance, populations of each cryptic wasp taxon will be absent from some locations when others are present. Two orchid taxa with different cryptic pollinators will each exclusively attract wasps at some locations. When such data are obtained, samples of the sibling wasp species are subjected to detailed examination of external morphology and genitalia by one of us (GRB) to determine whether any consistent differences in morphological characters occur.

Results

Initial pollinator choice tests attracted wasps, which appeared to conform with *Neozeleboria proxima* (Turner), to each of *Chiloglottis reflexa*, *C. trilabra* and *C. seminuda* (e.g., Experiment 1, Table 1). However, subsequent testing at a number of localities found that the *Neozeleboria proxima* sensu lato populations at some localities did not respond to one or two of the orchid taxa present (Experiments 4, 5, 6, 9 and 12, Table 1). This showed there were populations within *Neozeleboria proxima* s.l. which responded differentially to the odours emitted by the three orchid species, and suggested there may be cryptic taxa within *N. proxima*.

In addition, at two localities outside the normal range and habitats of *Chiloglottis seminuda* and *C. reflexa*, there were specific responses to each of the orchids by other easily distinguishable thynnine taxa. At Mullion Creek and Mt

Canobolas (Experiments 2 and 3, Table 1) *Asthenothynnus westwoodi* (Guérin-Ménéville) was uniquely attracted to *Chiloglottis seminuda*. On Mt Canobolas, *Neozeleboria* sp. nov. 25 was attracted to *Chiloglottis trilabra* and a species of *Eirone* Westwood to *C. reflexa* (Experiment 3, Table 1). These results showed the three orchid taxa had different pseudophoromones and supported their recognition as different species.

Close examination of the *Neozeleboria proxima* s.l. collections revealed consistent morphological differences among the populations responding to the three orchids. These differences are summarised in Table 2. The three wasp species are almost identical externally, with slightly more yellow on the two undescribed species, and morphological differences limited to the shape of the fore coxae and hypopygium (last visible sternite). The genitalia however, are distinctive and the three species are most readily and accurately determined from these.

In summary, the data in Table 1 show that *Chiloglottis trilabra* specifically attracted *Neozeleboria proxima* s.s. (131 exposures, 87 wasps caught) and *N. sp. nov. 25* (Mt Canobolas only, 5 wasps caught). *Chiloglottis seminuda* attracted *Neozeleboria* sp. nov. 29 (173 exposures, 74 wasps caught), but also attracted *Asthenothynnus westwoodi* outside its normal range (59 exposures, 29 wasps caught). *Chiloglottis reflexa* attracted *Neozeleboria* sp. nov. 30 (192 exposures, 124 wasps caught) in its normal habitats and an *Eirone* sp. outside its range at Mt Canobolas (14 exposures, 5 wasps caught).

Occasionally *Neozeleboria proxima* s.s. may respond weakly to *Chiloglottis reflexa* (Experiment 10, Table 1) (17 exposures, 2 wasps caught) and *C. seminuda* (unpublished data). These minor responses do not result in pollination (Bower, 1996) and indicate a slight similarity in pseudophoromones among the three orchid species, and possibly also the wasps.

Discussion

The experimental data presented above show that cryptic thynnine species can be detected by their specific attraction to particular sexually deceptive orchid species. The differential attraction is almost certainly based on differences in pseudophoromone chemistry between orchid species rather than appearance. Sexually deceptive orchids are therefore convenient sources of pheromones for studies of cryptic thynnine species. Due to their high attractiveness to

Table 1. Pattern of attraction of *Neozeleboria proxima* and its cryptic allies to *Chiloglottis reflexa*, *C. trilabra* and *C. seminuda* on the central coast and tablelands of NSW.

<i>Chiloglottis</i> species	Source of orchid	Thynnine species ¹	No. of wasps caught
Experiment 1: Mt. Wilson, 27 Feb 1993, 59 exposures, Sympatric test			
<i>C. trilabra</i>	Sunny Corner	<i>N. proxima</i>	51
<i>C. seminuda</i>	Mt Wilson	<i>N. sp. nov.</i> 29	26
<i>C. reflexa</i>	Mt Wilson	<i>N. sp. nov.</i> 30	14
Experiment 2: Mullion Creek, 13–14 Mar 1993, 45 exposures, Allopatric Test			
<i>C. trilabra</i>	Batlow	—	0
<i>C. seminuda</i>	Mt. Wilson	<i>A. westwoodi</i>	27
<i>C. reflexa</i>	Mt. Wilson	—	0
Experiment 3: Mt Canobolas, 13 Mar 1993, 14 exposures, Allopatric test			
<i>C. trilabra</i>	Batlow	<i>N. proxima</i>	24
		<i>N. sp. nov.</i> 25	5
<i>C. seminuda</i>	Mt Wilson	<i>A. westwoodi</i>	2
<i>C. reflexa</i>	Mt Wilson	<i>Eirone sp.</i>	5
Experiment 4: Nullo Mountain, 12 Apr 1993, 38 exposures, Allopatric Test			
<i>C. trilabra</i>	Serpentine NR	<i>N. proxima</i>	2
<i>C. seminuda</i>	Olinda	<i>N. sp. nov.</i> 29	24
<i>C. reflexa</i>	Nullo Mt.	—	0
Experiment 5: Mt Wilson, 18 Ap 1993, 21 exposures, Sympatric test			
<i>C. seminuda</i>	Nullo Mt	—	0
<i>C. seminuda</i>	Olinda	—	0
<i>C. reflexa</i>	Nullo Mt	<i>N. sp. nov.</i> 30	23
Experiment 6: Hartley Pass, 18 Ap 1993, 10 exposures, Sympatric test			
<i>C. seminuda</i>	Nullo Mt	—	0
<i>C. seminuda</i>	Olinda	—	0
<i>C. reflexa</i>	Nullo Mt	<i>N. sp. nov.</i> 30	6
Experiment 7: Mt Keira, Wollongong, 13 Feb 1994, 20 exposures, Sympatric test			
<i>C. seminuda</i>	Mt Keira	<i>N. sp. nov.</i> 29	2
<i>C. reflexa</i>	Mt Keira	<i>N. sp. nov.</i> 30	21
Experiment 8: Mt Keira, Wollongong, 13 Feb 1994. 15 exposures, Sequential test			
A ² . <i>C. seminuda</i>	Mt Keira	<i>N. sp. nov.</i> 29	7
B. <i>C. reflexa</i>	Mt Keira	<i>N. sp. nov.</i> 30	17

Table 1. Continued

Experiment 9: Jamberoo Mt, 14 Feb 1994, 6 exposures, Sympatric test

<i>C. seminuda</i>	Mt Keira	—	0
<i>C. reflexa</i>	Mt Keira	<i>N. sp. nov.</i> 30	9

Experiment 10: Macquarie Pass, Robertson, 14 Feb 1994, 17 exposures, Sympatric Test

<i>C. seminuda</i>	Mt Keira	<i>N. sp. nov.</i> 29	2
<i>C. reflexa</i>	Mt Keira	<i>N. sp. nov.</i> 30	27
		<i>N. proxima</i>	2

Experiment 11: Fitzroy Falls, 14 Feb 1994, 24 exposures, Sympatric Test

<i>C. seminuda</i>	Mt Keira	<i>N. sp. nov.</i> 29	13
<i>C. reflexa</i>	Mt Keira	<i>N. sp. nov.</i> 30	1

Experiment 12: Hartley Pass, 27 Feb 1994, 20 exposures, Sympatric Test

<i>C. trilabra</i>	Kanangra	<i>N. proxima</i>	10
<i>C. seminuda</i>	Mt Keira	—	0
<i>C. reflexa</i>	Mt Keira	<i>N. sp. nov.</i> 30	6

¹ *N.* = *Neozeleboria*, *A.* = *Asthenothynnus*

² A = Orchid species exposed alone in first 3 min. B = Orchid species added to the baiting array for the second 3 min.

Table 2. External morphological differences among *Neozeleboria proxima* and its sibling species.

Character	<i>Neozeleboria proxima</i>	<i>N. sp. nov.</i> 29	<i>N. sp. nov.</i> 30
fore coxa emarginate	weakly	not	strongly
hypopygium	triangular, not truncate	triangular, not truncate	subtriangular, truncate
parameres	long, curved	normal	normal
aedeagus	long	short	short
base of femora	black	orange	orange
anterior pronotum	black laterally	yellow laterally	yellow laterally
metasomal spots	reduced, yellow	not reduced, pale yellow	not reduced, pale yellow

thynnine males, they facilitate the collection of large samples for taxonomic study.

The apparent chemical basis for reproductive isolation in both cryptic *Chiloglottis* and pollinator species suggests that morphological and visual differences are of little or no importance in mate selection in thynnines and in their behaviour on the orchids they pollinate. Similarly, Paterson (1990) concluded that any group of organisms relying mainly on chemical or other non-visual signals for mate recognition is likely to contain cryptic species.

The selective attraction of thynnines by orchids has revealed significant diversity which may not have been detected by the alpha taxonomic approaches traditionally applied alone. Similar work still in progress has revealed other complexes of cryptic species in the Thynninae; among *Neozeleboria monticola* Turner and its allies, and in *Phymatothynnus monilicornis* (Smith). It is likely that a great deal more pheromone-based hidden biodiversity is present in thynnine wasps and, indeed, in other insect groups, e.g., moths (Mahon et al., 1982).

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References

- Bower, C.C., 1992. The use of pollinators in the taxonomy of sexually deceptive orchids in the subtribe Caladeniinae (Orchidaceae). *The Orchadian* 10: 331–338.
- Bower, C.C., 1996. Demonstration of pollinator-mediated reproductive isolation in sexually deceptive species of *Chiloglottis* (Orchidaceae: Caladeniinae). *Australian Journal of Botany* 44: 15–33.
- Drew, R.A.I. and Hardy, D.E., 1981. *Dacus (Bactrocera) opilliae*, a new sibling species of the *dorsalis* complex of fruit flies from northern Australia (Diptera: Tephritidae). *Journal of the Australian Entomological Society* 20: 131–137.
- Handel, S.N. and Peakall, R., 1993. Thynnine wasps discriminate among heights when seeking mates: tests with a sexually deceptive orchid. *Oecologia* 95: 241–245.
- Jones, D.L., 1988. *Native orchids of Australia*. Reed Books: Frenchs Forest.
- Mahon, R.J., Miethke, P.M. and Mahon, J.A., 1982. The evolutionary relationships of three forms of the Jarrah Leaf Miner, *Perthida glyphopa* (Common) (Lepidoptera: Incurvariidae). *Australian Journal of Zoology* 30: 243–49.
- Paterson, H.E.H., 1990. The recognition of cryptic species among economically important insects. Pp.1–10 in: Zalucki, M.P. (ed), *Heliothis: research methods and prospects*. Springer-Verlag: New York.
- Paulus, H.F. and Gack, C., 1990. Pollinators as pre-pollinating isolation factors: evolution and speciation in *Ophrys* (Orchidaceae). *Israel Journal of Botany* 39: 43–79.
- Peakall, R., 1990. Responses of male *Zaspilothynnus trilobatus* Turner wasps to females and the sexually deceptive orchid it pollinates. *Functional Ecology* 4: 159–167.
- Peakall, R. and Handel, S.N., 1993. Pollinators discriminate among floral heights of a sexually deceptive orchid: implications for selection. *Evolution* 47: 1681–1687.
- Stoutamire, W.P., 1974. Australian terrestrial orchids, thynnid wasps and pseudocopulation. *American Orchid Society Bulletin* 43: 13–18.
- Stoutamire, W.P., 1975. Pseudocopulation in Australian terrestrial orchids. *American Orchid Society Bulletin* 44: 226–233.
- Stoutamire, W.P., 1983. Wasp-pollinated species of *Caladenia* in south-western Australia. *Australian Journal of Botany* 31: 383–394.
- Stoutamire, W.P., 1986. *Spiculaea ciliata*, the Australian elbow orchid. *Canadian Orchid Journal* 3: 19–23.
- Whittle, C.P., Bellas, T.E., Horak, M. and Pinese, B., 1987. The sex pheromone and taxonomic status of *Homona spargotis* sp. rev., an Australian pest species of the *Coffearia* group (Lepidoptera: Tortricidae: Tortricinae). *Journal of the Australian Entomological Society* 26: 169–179.

A CONSERVATION ASSESSMENT OF THE AQUATIC MACROINVERTEBRATE FAUNA IN THE GRAMPIANS NATIONAL PARK

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Abstract

Doeg, T.J., 1997. A conservation assessment of the aquatic macroinvertebrate fauna in the Grampians National Park. *Memoirs of the Museum of Victoria* 56: 467-473.

A total of 236 aquatic macroinvertebrate taxa were identified at 32 riverine sites in the Grampians National Park. At least 23 of the taxa may represent species restricted to the park. The genus *Austrophlebioides* (Ephemeroptera, Leptophlebiidae) was missing from all sites surveyed, despite suitable habitat. Ordination indicated three distinct groups of sites within the park, primarily based on the stream-bed substrate type. Standard conservation measures were attempted (diversity, uniqueness, rarity, etc) with limited success. Twenty sites showed some characteristics of conservation significance. One site was shown to be more diverse than all others, six sites had more than three endemic species present, seven sites had the only record of an endemic species, the Mackenzie River was shown to be a unique area in the park (with an associated distinct fauna) and other sites scored highly on statistical conservation indices. None of the conservation measures used could, by themselves, identify all the significant sites within the park.

Introduction

Traditional methods of assessing the conservation status of riverine sites revolve primarily around the lack of human disturbance at a particular site or within a catchment (Mitchell, 1990) or are based on the presence of species with high conservation status (e.g., CNR, 1995). However, assessments of the 'naturalness' of individual sites or catchments do not necessarily translate immediately to the equivalent significance for the invertebrate community. Meredith et al. (1989) evaluated stream segments in East Gippsland according to the presence of impoundments, in-stream works, pollution sources, roading, and the percentage of timber harvesting and non-native vegetation. However, the impact of these disturbances is site dependant and such a simplistic evaluation may not reflect the impact on the fauna. In fact, patterns in the aquatic macroinvertebrate fauna of the area (derived from multivariate groupings) do not correspond to the on-ground patterns derived from 'naturalness' evaluation (T. Doeg, Freshwater Ecology Section, unpublished data).

Where individual species are used to identify sites of significance, the identification of the species of conservation significance is often based on a well established knowledge of both the taxonomy and distribution of certain groups of flora and fauna (e.g., fish). However, knowl-

edge of the taxonomy and distribution of aquatic macroinvertebrates is not sufficiently detailed in Victoria to allow correct assignment of a conservation status (e.g., Doeg and Reed, 1995). Yen and Butcher (1994) suggest that single species conservation may be inappropriate for the majority of invertebrates and that other techniques or criteria should be applied. These include habitat-based or community-based approaches.

A number of alternative methods have been suggested for these other approaches. This paper evaluates some of these methods, using data collected as part of a National Estate survey of streams in the Grampians National Park.

Methods

A total of 60 sites was sampled (Fig. 1) throughout the Grampians National Park from all major drainage areas. Sites ranged from wide vegetation-choked channels, small slow-flowing silty tributaries, faster flowing sand to cobble bed streams to steep boulder dominated rivers. At each site, standardised kick samples were collected from the main channel using an FBA net (150 μ m mesh net). Macroinvertebrates were picked from a one-tenth subsample and identified. The funding provided for this project allowed only 32 sites to be completed (Fig. 1). Samples from the remaining sites are currently being processed and a full analysis of the results,

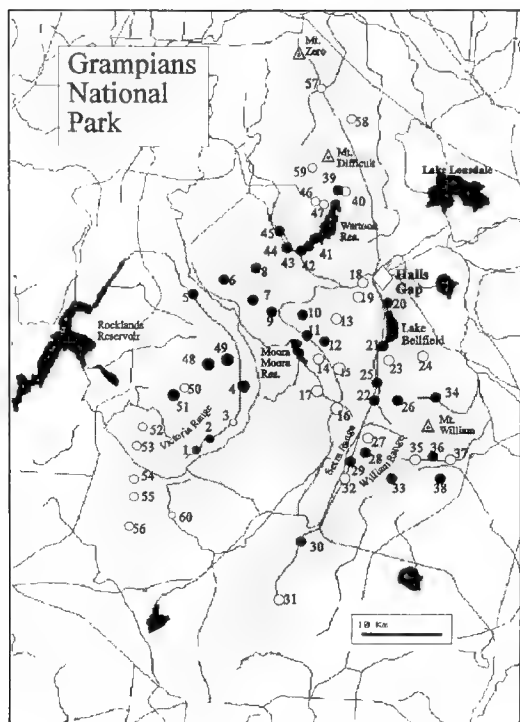


Figure 1. Map of the study area showing the location of sampling sites. l — sites processed during this study; m — sites sampled but not processed during this study.

including the species collected will be presented elsewhere.

Conservation analysis

The traditional conservation analysis of using land use characteristics to identify significant sites (Meredith et al., 1989) should, in fact, eliminate much of the Grampians National Park from a high conservation rating. The presence of major reservoirs (Lake Wartook and Moora Moora Reservoir), the extensive networks of roads and tracks, historical grazing and timber harvesting would automatically reduce the value of most park streams. Despite this, the LCC identified the Victoria Range, Serra Range and the Major Mitchell Plateau as having Remote and Natural attributes worthy of note (LCC, 1991).

No previous attempt has been made to assess the conservation status of the Grampians in terms of the aquatic macroinvertebrate fauna. Suggested methods of using freshwater macroin-

vertebrates in conservation analysis fall into five main types — diversity, presence of rare and endangered species, presence of local endemic species, groupings of sites with distinct community compositions, and proposed statistical tests of rarity.

Diversity patterns

Generally, sites are considered to be of significance based on diversity measures if they have a large number of species present, or more correctly, a higher number of species present than would be expected. There are insufficient data on the Victorian fauna to establish (in a formal sense) the expected number of species at any particular site. Current work elsewhere under the River Health Initiative is attempting to produce a predictive model, where the likely composition and diversity of a site can be estimated from a series of environmental variables.

However, diversity measures alone may not always indicate the true nature of the site. Numerous examples exist where clearly disturbed sites are not distinguished from undisturbed sites, based simply on the number of taxa present (e.g., Doeg, 1985).

In an overall sense, the 236 taxa of freshwater macroinvertebrates recorded at the 32 sites compares favourably with other intensive surveys in Victoria. For example, in East Gippsland, similar kick samples collected at 48 sites resulted in 269 taxa (T. Doeg, unpublished data) while similar orders of total diversity have been recorded in the upper Goulburn River (Doeg 1985), the Thomson River (Doeg et al., 1987), the Yarra River (Pettigrove 1989) and the Latrobe River (Metzeling et al., 1984). Care should be taken in comparing regional diversity between surveys due to differences in the distribution of site characteristics, sampling methods and taxonomic discrimination, but there is no reason to suspect that the total fauna collected was any more or less diverse than other aquatic sites sampled throughout Victoria.

The number of taxa found at each site (from 8 to 72) was broad (Fig. 2). The site with the highest number of taxa was at Site 21 on Fyans Creek on the Grampians Tourist Road (72 taxa). This was substantially higher than any of the other sites, the site with the nearest diversity, also on Fyans Creek, having only 56 taxa.

Rare, endangered and endemic species

The presence of rare and endangered species is a valid determinant of high conservation status. However, the lack of adequate taxonomic and

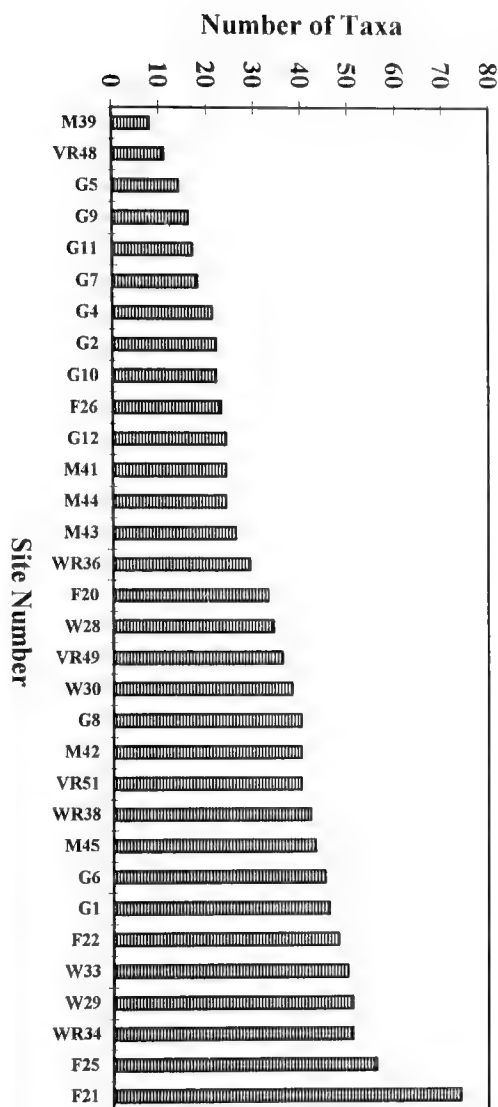


Figure 2. Number of taxa recorded at each site, sorted from lowest to highest. Numbers from Fig. 1 with reference to the following catchments: G — Glenelg; F — Fyans Creek; W — Wannon River; WR — Mt William Range; M — McKenzie River; VR — Victoria Range.

distributional knowledge restricts our ability to identify species that are truly rare or restricted (Butcher and Doeg, 1995). However, no taxon present on the official lists of rare and endangered species (CNR, 1995) was located in this survey. Given the paucity of sampling conducted previously in the Grampians, it is not surprising that rare or endangered species described from elsewhere in the state were not located there.

The majority of species collected have been recorded in other work in other places in Victoria. Significantly, 23 of the taxa (10% of the fauna) were identified as either unrecorded in recognised voucher collections, or as distinct from a known or described species, and may be new species restricted to the Grampians (herein called 'endemic' taxa). As such, they fall into the category of having limited distributions and could possibly qualify for inclusion in lists of rare species. The unique nature of the Grampians biota revealed in both flora and vertebrate surveys is therefore also reflected in the presence of a large proportion of new and possibly endemic freshwater taxa.

Twenty seven of the 32 sites processed contained at least one endemic taxon. The most number of such taxa at a single site was 6, at Site 6, an un-named tributary of the Glenelg River on Hines Track. Nine of the potential endemic taxa were located at single sites within the park.

Of particular interest, the major genus of mayfly, *Austrophlebioides*, was absent from any of the sites sampled. *Austrophlebioides* is common on rocks in stony upland streams but 'are not commonly found at lowland sites or sandy sites' (Marchant et al., 1994), and are often reduced in abundance due to the impact of human disturbance (Doeg, 1985, Doeg and Koehn 1994). However, members of the genus are known throughout Victoria at almost all altitudes, and often form a significant component of the freshwater fauna. Even in some of the more disturbed streams, such as the Mitta Mitta River in north-east Victoria (Blyth et al., 1984), *Austrophlebioides* were still located, albeit in reduced numbers. While it is not unreasonable for the genus to be absent from the silt or sand-based sites, many other sites had conditions suitable for the taxon (particularly at cobble sites). Given the number of sites sampled, the genus should have been located if it was present. Either it has never been present in the Grampians, or some (possibly natural or cyclical) event in the past has lead to its elimination.

Site groupings

The use of multivariate analyses can enable the identification of distinct groupings of sites that have a distinctive fauna within a small geographic area, like the Grampians. Classification by TWINSpan indicated the formation of 4 distinct groups of sites (Fig. 3). The first division, indicating the most distinct group (Group 1), separated a group of 7 sites on the Glenelg River and one site on the McKenzie River upstream of Wartook Reservoir. Seven of the Group 1 sites were those with predominantly silt and/or vegetation substrata. Unusually, Site 12 (Moor Creek) has a substrate of cobbles and boulders, but a nearby parallel road, suggesting a sedimentation impact.

Even though the majority of Group 1 sites were located in the Glenelg River catchment, other sites (that have not been processed yet) with similar substrates can be found in other catchments in the park. Hence, the separation of the Group 1 probably reflects the distribution of a habitat-type and not a particular area of significance.

The second major division separated the sites on the McKenzie River downstream of the Wartook Reservoir from all of the other sites (Group 2). These sites were in a high gradient, high flow stream, generally with the highest proportion of larger particle sizes (cobbles through to boulders). This division is of more significance, as while this may also be substrate based, there are no similar habitats within the park, and similar faunal compositions at sites outside the McKenzie River catchment are unlikely to be found. Thus, the McKenzie River downstream of Lake Wartook may be seen as an area of some local conservation significance (despite the presence of the reservoir upstream).

Group 3 contained sites on Fyans Creek and the Wannon River (substrates composed primarily of cobbles), with Group 4 comprised of

all the remaining sites primarily with a sand or pebble component (mainly the Glenelg River, and William and Victoria Range sites). Such sites are widespread throughout the park.

In general, ordination by Reciprocal Averaging (Fig. 4) reflected the major groupings outlined by the classification, but with little discrimination between the mixed substrata sites. Significantly, the ordination indicated that the community composition at Site 43 (located immediately below a popular tourist complex with a defective sewage system) was distinct from the remaining Mackenzie River sites, which showed a higher degree of similarity. Site 43 was not clearly distinct from the other sites on the basis of diversity measures alone (a total of 26 taxa compared to 24–43 at the other sites in the group), but had a distinctly disturbed fauna dominated by oligochaetes and chironomids.

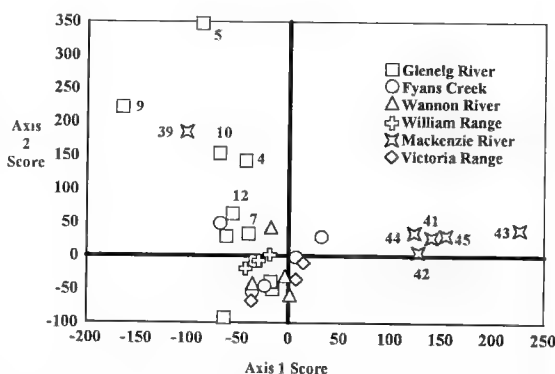


Figure 4. Reciprocal Averaging (RA) plot showing the relationship between sites. Only site numbers for Groups 1 and 2 from the TWINSpan analysis are shown.

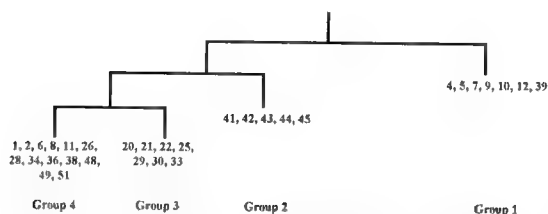


Figure 3. TWINSpan dendrogram showing the relationship between sites and site groupings. Numbers as for Fig. 1.

Rarity measures

While the techniques or measurements employed to evaluate conservation significance above are relatively widespread and accepted, the evaluation of freshwater macroinvertebrate communities using statistical indices does not appear to have been used for freshwater macroinvertebrates in Victoria or Australia. Such indices were developed to enable an objective assessment of site values, free from the drawbacks of more subjective value judgements.

Objective tests on conservation criteria were based on the methods described in Eyre and

Rushton (1989). Each of the 236 taxa was assigned a score on a geometric scale (1–16) based on the number of sites out of the 32 at which it was collected, awarding higher scores to species occurring at fewer sites. The highest score (16) was assigned to species occurring at only one of the sites sampled, with 8 points to species occurring at 2–4 sites, 4 to species at 4–7 sites, 2 to species at 8–15 sites and 1 to species at 16–32 sites.

A site score (termed the Species Rarity Total — SRT) was calculated as the simple sum of all the scores of all the species present at the site. Each of the SRT indices were divided by the number of species at each site to obtain a second site score, the Species Quality Factor (SQF). The SRT and SQF were graphed and analysed by eye to detect sites of outlying low or high rarity values.

While such indices have some appeal as a simple estimate of site significance, it is important to understand exactly what the indices reflect. The SRT is a simple sum of the individual species score, so that a site with many rare species scores higher than a site with fewer rare species.

However, the SRT score will also be affected by the total number of taxa, so that a site with many taxa will score higher than a site with fewer taxa, even if they have the same number of rare or restricted species. This is demonstrated in the present case. Site 21 clearly had the highest values for SRT (Fig. 5) of all the sites examined. This site also had the highest number of taxa of any site. But that site did not have the highest number, or proportion, of taxa unique to that site. There were 6 taxa found only at Site 21 (8.3% of the total at the site), the same number as Site 8 (6 out of 40 taxa, 15% of the total), but this is compared with 9 at Sites 6 (44 taxa, 20%) and 30 (38 taxa, 23%). Site 9 had 5 unique taxa (representing 31% of the 16 taxa collected, the highest proportion of all sites).

While Sites 6 and 30 had the second and third highest SRT respectively, Site 8 was ranked sixth, and 9 was ranked 15th among all the sites. Hence, the calculation of SRT values does not seem to reflect all the possible criteria that could be used to determine the rarity of a site.

The Species Quality Factor (the SRT divided by the number of taxa) overcomes many of the problems of using the raw score. By standardising the score, the SQF more reflects the proportion of taxa at a site that are rare. Hence, Sites 9, 30, 5 and 6 all score highest, in that order (Fig. 6), in this calculation reflecting the proportion of

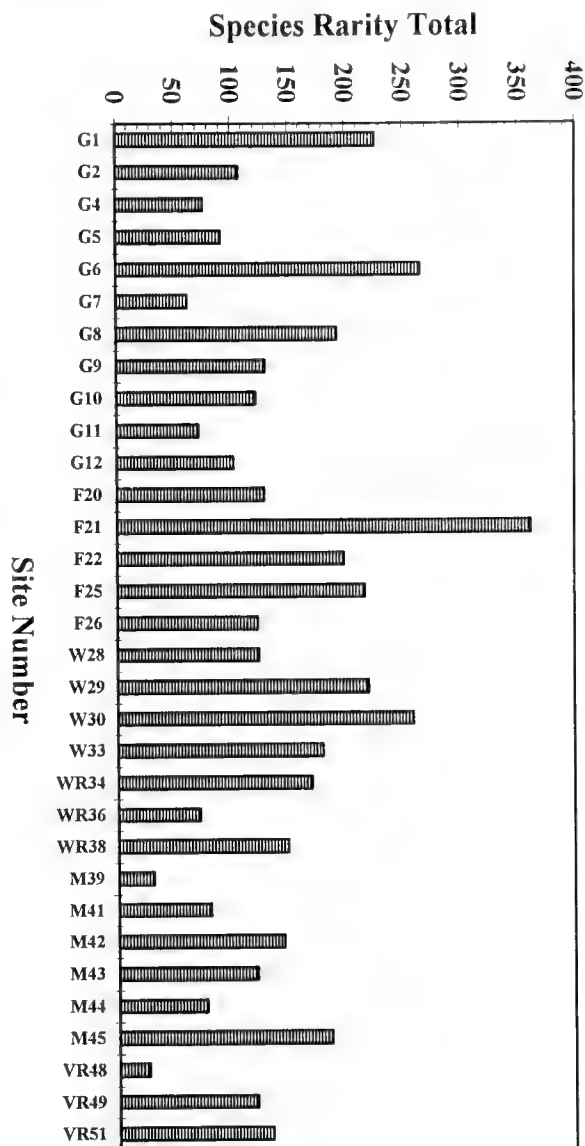


Figure 5. Species Rarity Total for each site.

unique taxa (31%, 23%, 21% and 20% respectively — the four highest proportions of all sites). This provides a more intuitively satisfying solution to the use of indices, downplaying the presence of common taxa and identifying sites with the largest proportion of the fauna composed of restricted taxa.

Conclusions

Depending on the type of measure used, twenty sites with some significance status could be identified (Table 1). One site was shown to be more diverse than all others, six sites had more

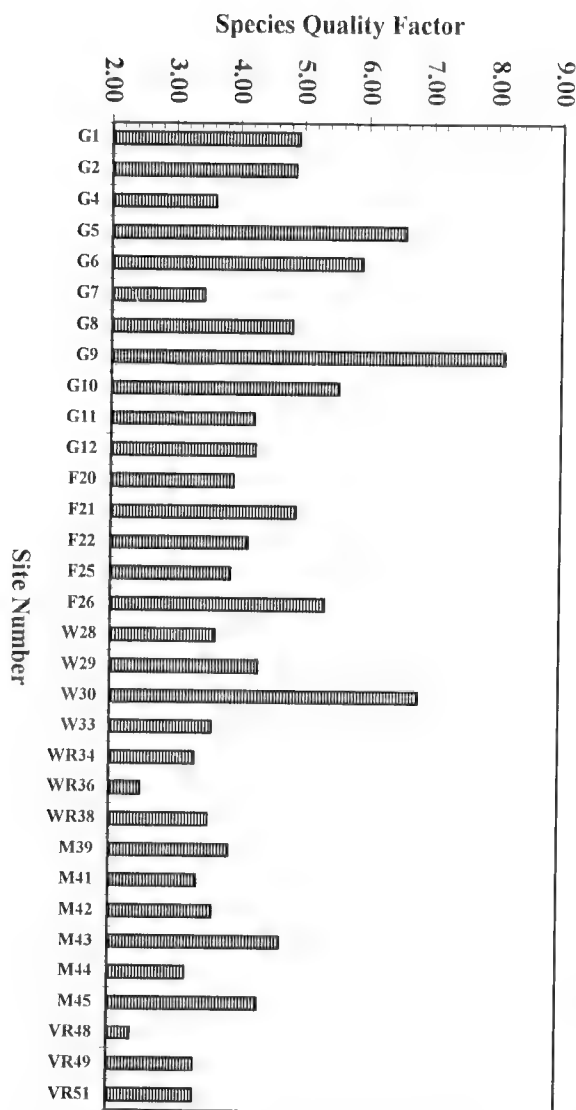


Figure 6. Species Quality Factor for each site.

than 3 endemic species present, seven sites had the only record of an endemic species, the Mackenzie River was shown to be a unique area in the park (with an associated distinct fauna) and other sites scored highly on statistical indices. None of the conservation measures used could, by themselves, identify all of the sites within the park with characteristics of conservation significance. It is clear that for aquatic macroinvertebrates to be used to identify areas or sites of conservation significance, far more information on the characteristics of natural undisturbed communities needs to be collected.

References

- Blyth, J.D., Doeg, T.J. and St Clair, R.M., 1984. Response of the macroinvertebrate fauna of the Mitta Mitta River, Victoria, to the construction and operation of Dartmouth Dam. 1: Construction and initial filling period. *Occasional Papers from the Museum of Victoria* 1: 83-100.
- Butcher, R. and Doeg, T., 1995. Conservation of freshwater invertebrates. *Victorian Naturalist* 112: 15-19.
- CNR, 1995. *Threatened fauna in Victoria — 1995*. Department of Conservation and Natural Resources: Victoria.
- Doeg, T.J., 1985. Macroinvertebrate communities in the Goulburn River and tributaries above Lake Eildon, Victoria. *Bulletin of the Australian Society for Limnology* 11: 47-61.
- Doeg, T.J. and Koehn, J.D., 1994. Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. *Regulated Rivers* 9: 263-277.
- Doeg, T. and Reed, J., 1995. Distribution of the endangered Otway stonefly *Eusthenia nothofagi* Zwick (Plecoptera: Eustheniidae) in the Otway Ranges. *Proceedings of the Royal Society of Victoria* 107: 45-50.
- Eyre, M.D. and Rushton, S.P., 1989. Quantification of conservation criteria using invertebrates. *Journal of Applied Ecology* 26: 159-171.
- LCC, 1991. *Wilderness: Special Investigation. Final Recommendations*. Land Conservation Council, Victoria.
- Marchant, R., Barmuta, L.A. and Chessman, B.C., 1994. Preliminary study of the ordination and classification of macroinvertebrate communities from running waters in Victoria, Australia. *Australian Journal of Marine and Freshwater Research* 45: 1-18.
- Meredith, C., Goss, H. and Seymour, S., 1989. *Nature conservation values of the rivers and catchments of Gippsland*. Report No. 44. Department of Water Resources, Victoria.
- Metzeling, L., Graesser, A., Suter, P. and Marchant, R., 1984. The distribution of aquatic macroinvertebrates in the upper catchment of the Latrobe River, Victoria. *Occasional Papers from the Museum of Victoria* 1: 1-62.
- Mitchell, P.A., 1990. *The environmental condition of Victorian streams*. Department of Water Resources, Melbourne.
- Pettigrove, V.J., 1989. *Biological monitoring of the Yarra River using macroinvertebrates*. Scientific Report Series No. 88/104. Environment Protection Authority, Victoria.
- Yen, A. and Butcher, R., 1994. *An overview of the conservation status of non-marine invertebrates in Australia*. Endangered Species Unit and Australian Nature Conservation Agency, Canberra.

Table 1. Summary of sites displaying some degree of uniqueness based on each of the types of analysis used in this report.

Site	Diversity	Endemic species present	Only site for endemic species	Members of distinct group	SRT	SQF
1					4	
2			1			
5						3
6		6	2		2	4
8			1			
9			2			1
10			1			
11						
21	+	4	1		1	
25		5				
30					3	2
33		4				
34			1			
36		4				
41-45				+		
49		4				

Explanation of codes: *Diversity* — The site with the highest number of taxa; *Endemic species present* — More than 3 possible endemic species present; *Only site for endemic species* — Number of local taxa restricted to only that site; *Members of distinct group* — Mckenzie River sites; *Rarity SRT* — Top four ranked scores for Species Rarity Total; *Rarity SQF* — Top four ranked scores for Species Quality Factor.

INVERTEBRATE FAUNA OF THE TAMAR ESTUARY, NORTHERN TASMANIA

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Abstract

Smith, B.J., 1997. Invertebrate fauna of the Tamar estuary, northern Tasmania. *Memoirs of the Museum of Victoria* 56(2): 475-482.

There are very few large estuaries in southern Australia. One of the most significant is the Tamar Estuary in northern Tasmania, capable of admitting 80 000 ton ships into its lower reaches and navigable by ships of over 4000 tons to the City of Launceston more than 60 km from Bass Strait. Estuaries are the most heavily utilised and modified of all coastal habitats. The habitat range within a large estuary is wider than any other aquatic habitat, being subject to three sets of variables: habitat type (from rocky shore to soft mud), extent of tidal exposure and salinity. Thus, while the species of intertidal animals inhabiting estuaries are amongst the most tolerant of environmental change, they are also the most threatened of littoral assemblages. Although the Tamar Valley was settled by Europeans over 190 years ago and the estuary services a large city, intensive agriculture and heavy industry, the fauna still has most of the assemblages expected in a large estuary. Results of a distributional survey of the intertidal invertebrate fauna of the Tamar are presented and comparisons made with other major estuaries in southern Australia.

Introduction

All intertidal animals live in a habitat subject to two sets of environmental variables: the various substrate types and the rise and fall of the tides. The estuarine intertidal environment has a third habitat variable, salinity, in addition to these. Thus intertidal estuarine species are amongst the most tolerant of environmental fluctuations of any assemblages of animals. Many of the species of invertebrates that live in a large estuary have populations which, over a typical annual cycle, are subject to wide daily and seasonal variations in flow, salinity, suspended solid load, temperature and many other factors. The species that can tolerate such fluctuations are few in number but often have very large population densities as competitors are also few in number.

Unfortunately the geographical characteristics of large estuaries also make them very attractive for human development. Many around the world are sites for major cities, massive port construction and the development of heavy industry on flat land close to large-ship access, often with resultant massive habitat change and heightened pollution of the waterway. Large estuaries are those whose inflow rivers have large catchments and wide deep entrances that allow significant tidal inflow. They also have a significant longitudinal zone of tidal influence that allows the development of a gradual salinity gradient.

By this definition there are very few major estuaries in the southern Australian faunal zone. Virtually none of the rivers of Victoria, South Australia or the southern coast of Western Australia have the series of characteristics that would enable them to be classified as major estuaries. They mainly lack a significant longitudinal distance of tidal influence and hence a gradual salinity gradient. In most of these mainland southern rivers the zone of reduced salinity is comparatively short, only a kilometre or two at most. Tasmania has three or four estuaries which might be classified as major: Bathurst and Macquarie Harbours on the west coast, the Derwent River in the south east and the Tamar River on the north coast. Of these the Tamar is the largest and the only one with an extensive central section which is truly estuarine in character.

The Tamar is the tidal estuary of the North Esk and South Esk Rivers, which combine at the site of the City of Launceston. From here the estuary runs NNE for about 63 river km to Bass Strait. The tidal range is approximately 3 m at George Town near the mouth and 3.5 m at Launceston (Phillips, 1975; Pringle, 1982). Bottom salinity values vary in a regular manner from normal marine (about 35.3 parts per thousand) in Port Dalrymple to about 18 ppt at Dilston, to almost fresh (less than 1 ppt) at Launceston in both summer and winter (Bell, in press). The freshwater inflow from the two rivers can fluctuate

tuates widely over a year with occasional major floods.

The Tamar Valley was first settled by Europeans in 1804 and is now a major centre of population, trade and commerce with a population of over 100 000 people. A great deal of dredging, removal of hazards and other 'improvements' have been carried out over the years so that ships of over 4200 tons are able to reach Launceston, while the berths at Bell Bay in Port Dalrymple take ships of over 80 000 tons (Branagan, 1994). Heavy industry has been established along the lower reaches close to these major port facilities.

Besides all the 'river improvements' and development that have so changed the character of the estuary, two organisms introduced into the Tamar in the last 50 years, have had a profound effect on its appearance and biology. The exotic Rice-Grass, *Spartina anglica*, was introduced into the Tamar at Windermere in 1947 by the Marine Board and the Department of Agriculture to stabilise the mudflats and eventually turn them into 'useful land', and to force the stream flow into the central part of the estuary, creating a scouring effect and keeping the main channel free of mud. *Spartina anglica* now covers over 500 ha in the estuary and stretches from south of Tamar Island to north of East Arm (Phillips, 1975; Pringle, 1993).

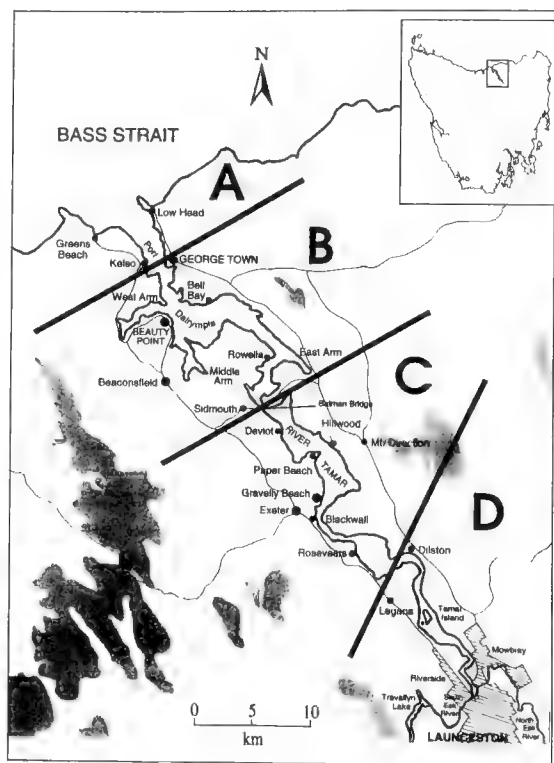
The Pacific Oyster, *Crassostrea gigas*, was introduced into Port Sorell, northern Tasmania by CSIRO in 1953 in an attempt to start an oyster industry. It is thought that introductions from this source into the Tamar took place fairly rapidly by natural transport of planktonic larvae by coastal currents. This species is now massively established in the Tamar forming a heavy band about the mid tide level and providing hard substrate for the settlement of other animals in places where very little occurred naturally (Thomson, 1959; Coleman, 1986; Olsen, 1994). The oyster now occurs over three-quarters of the length of the estuary from George Town to Freshwater Point.

Survey of common intertidal macroinvertebrates

No comprehensive survey has ever been carried out of the invertebrate fauna of the entire estuary. A number of small, local studies have been done in specific areas of planned development but many of these have never been published. To provide some baseline data on the fauna of the whole estuary and to make an assessment of its

health, a distributional survey of the common intertidal macroinvertebrates of the Tamar was carried out during 1993–1994. The area of the estuary was divided into 2 x 2 km squares and each square was visited as access permitted and observations and basic collections of specimens were made. Each square was visited at least once and several squares in critical areas were visited a number of times to cover all the main habitat types. All specimens collected were identified and incorporated into the research reference collections of the Queen Victoria Museum. The results were tabulated and an assessment made of the fauna.

From an assessment of the distribution of the intertidal invertebrates found on the survey the estuary was divided into four zones (Map 1). Zone A extended from Low Head to George Town; Zone B from George Town to the Batman Bridge; Zone C from the Batman Bridge to Dilston and Zone D from Dilston to Launceston. Zone A yielded a wide diversity of species typical of the sheltered open coast fauna found right



Map 1. Map of the Tamar Valley showing the main geographical features (the four faunal zones — A, B, C, D — are shown) (shaded areas are high ground).

along the north coast of Tasmania and almost identical to that described for the Victorian coast by the Marine Research Group of Victoria (1984). Species that were only found in this zone in the survey are not listed in the detailed results of the survey below as they are not considered to be species inhabiting the estuary.

Species found in any of the other three zones are listed in Appendix 1. A summary of the species numbers in each major group of invertebrates is given in Table 1. Distribution maps of 28 of the commonest species are published elsewhere (Smith, 1995).

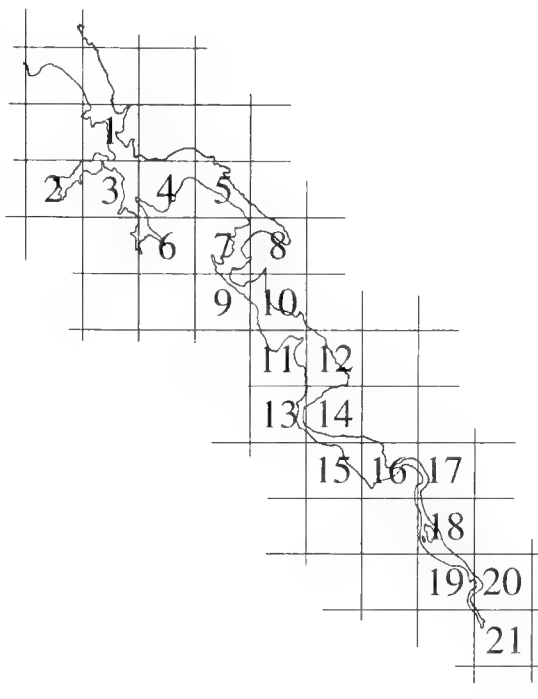
Many of the smaller or the more uncommon species are not listed here. In particular the polychaete, isopod and amphipod species numbers are probably significantly under represented as their habitats were not thoroughly searched. Some sieving and microscope examination of debris samples was carried out but the main field technique used was hand searching and picking.

A more detailed summary of the distribution of the commoner species is given in Appendix 2. For this, data from the original 2 x 2 km squares are amalgamated into 4 x 4 km squares beginning at the Zone A/Zone B boundary. The distribution of these large squares on an outline of the Tamar is given in Map 2. Thirty-three of the larger and more common species are listed with their presence in the larger squares marked. The total number of species for each large square is given. Zone B consists of squares 1 to 8; Zone C squares 9 to 16; Zone D squares 17 to 21.

Of the 33 species considered for this analysis, Zone B has an average of 21 species per square; Zone C has 12.5 and Zone D has 3. In Zone B, square 1 is the area closest to fully marine conditions with by far the highest number of species recorded. By contrast, square 2, with only 16 species, is the at the end of West Arm, far away from the main channel. Squares 9 and 10 have the highest species count in Zone C, being the closest to Zone B. There is a significant drop in the number of species recorded in the transition between Zones C and D (squares 16 and 17).

Discussion

The large and varied intertidal fauna found between Low Head and George Town was in every way typical of the fauna of comparable habitats anywhere along the open Bass Strait coast. After the study was completed, the ore carrier, *Iron Baron*, ran aground in July 1995 off the mouth of the Tamar, causing a major oil spill



Map 2. Map of the Tamar with the 4 x 4 km grid squares used in Appendix 2.

which grossly affected this fauna. Damage was caused both by the oil and by the physical and chemical means used to 'clean up' the spill from the intertidal zone. While the local damage was severe, it is anticipated that this event will have little or no long-term effects as recolonization should take place via planktonic larvae from adjacent areas within one or two seasons.

Major elements of this open coast fauna extend some distance up river beyond George Town at least into the Port Dalrymple-Bell Bay basin (Appendix — Zone B). More detailed work would reveal how much of this fauna is self-perpetuating, recruiting the next generation from within the area, and how much is accidental, developing from planktonic larvae carried into the estuary by tidal currents from breeding populations along the coast. Certainly many of the species are only found on, or close to, the main channel; the narrows between Point Effingham and Clarence Point are especially rich in open coast species. Species such as the rocky shore limpet, *Cellana tramoserica*, were found at Point Effingham but no further into the estuary. Once through these narrows the tidal current enters the broad expanse of Port Dalrymple and it can be surmised that many of

the larvae of the open coast species are no longer able to find favourable settling sites.

The wide area of Port Dalrymple, with its almost full sea-water salinity and variety of habitat types, has a broad diversity of faunal assemblages, even though it also carries major port development, and the sediment may be contaminated with heavy metals from old mining tailings and the discharge of industry. The mud-dwelling species reach their largest numbers in this region of quiet sheltered waters. These include the burrowing bivalves *Spisula* (*Notospisula*) *trigonella*, *Katelysia peronii* and *Eumarcia fumigata*, with *Laternula* spp. and *Thraciopsis elongata* in the soft mud areas. These latter species were found together with a variety of polychaetes, the mud crab *Heloeius cordiformis*, and a callinassid shrimp *Callinassa ceramica*.

South of Batman Bridge the estuary becomes more estuarine in character with a lower salinity and a much simpler intertidal fauna which lacks many of the open coast species (Appendix — Zone C). This pattern is mirrored in recent work on the Foraminifera of the estuary (Bell, in press). The species that persist in this zone obviously have a wider habitat tolerance than their fully marine relatives, since they are able to live not only with greater fluctuations in salinity but also higher silt loads in the water, and a negligible input of ocean plankton carried in on tidal currents. There is still a strong tidal influence in this region but far less tidal input or flushing. Despite the conditions this zone still yielded 50 species of intertidal invertebrates (Table 1), even 25 km or more from Bass Strait.

This central part of the estuary is dominated by two introduced organisms, the Rice Grass, *Spartina anglica*, and the Pacific Oyster, *Crassostrea gigas*. The extent and effects of the *Spartina* infestation was documented recently by Pringle (1993). A species that was once widely introduced as an aid to land reclamation and prevention of coastal erosion in many parts of southern Australia and New Zealand, *Spartina* is now being viewed as an environmental problem. The Pacific Oyster has the largest biomass of any intertidal animal in the estuary. Another exotic species was recognised as a recent introduction into the estuary. The small bag mussel, *Musculista senhousia* (Benson, 1842) was recorded from the Tamar for the first time. It has been recorded as an introduction into New Zealand (Willan, 1985) and the Swan Estuary, Western Australia (Slack-Smith and Brearley, 1987). Since then it has been recorded from Port Phillip

Bay (R. Burn, pers. comm.). A native of the western North Pacific, it is one of the species thought to have been introduced world-wide in ballast water. Other introduced ballast water species, such as the Northern Pacific Seastar, *Asterias amurensis*, now infesting the Derwent Estuary in southern Tasmania may establish themselves in the Tamar in the future.

South of Dilston (Appendix, Zone D) the intertidal fauna becomes extremely simple with only 11 species being found. These comprise 4 gastropods, 4 crabs, 1 shrimp, 1 bivalve and 1 worm species. Though still being fully tidal, the water has a greatly reduced salinity and a heavy silt load.

The presence of these varied faunal assemblages over the whole length of the estuary suggests that, despite all the developments and improvements carried out over the more than 190 years of European use of the river, the overall health of the river appears to be good. Other estuaries within the southern Australian faunal region have similar suites of species. The molluscs of some of the larger estuaries in southwestern Australia were listed by Wells (1984) but most of these estuaries were much smaller in size, and especially in longitudinal extent, than the Tamar. The Derwent is similar in some respects to the Tamar, but is more heavily affected by discharge from the city and industry of Hobart and also has a much shorter estuarine segment where the salinity is reduced.

References

- Bell, K.N., 1996. Foraminiferan fauna of the Tamar River and Port Dalrymple, Tasmania: a preliminary survey. *Records of the Queen Victoria Museum* 102: 1–25.
- Branagan, J.G., 1994. *The historic Tamar Valley — its people, places and shipping 1798–1990*. Launceston: Regal Publishing. 316 pp.
- Coleman, N., 1986. A review of introductions of the Pacific Oyster (*Crassostrea gigas*) around the world and a discussion of the possible ecological consequences of introducing the species into Victoria, Australia. *Department of Conservation, Forests and Lands, Victoria Technical Report* 56. 39 pp.
- Marine Research Group of Victoria, 1984. *Coastal invertebrates of Victoria: an atlas of selected species*. Museum of Victoria: Melbourne. 168 pp.
- Olsen, A.M., 1994. The history of the development of the Pacific Oyster, *Crassostrea gigas* (Thunberg) industry in South Australia. *Transactions of the Royal Society of South Australia* 118(4): 253–259.

Table 1. Summary of the numbers of species of intertidal macroinvertebrates collected in each of the zones of the Tamar.

Invertebrate Group	Zone B	Zone C	Zone D
Porifera	3	2	—
Cnidaria — Actinaria	1	—	—
Platyhelminthes — Polycladida	1	—	—
Bryozoa	3	1	—
Annelida — Oligochaeta	—	—	1
Annelida — Polychaeta	15	4	—
Mollusca — Polyplacophora	6	1	—
Mollusca — Bivalvia	20	7	1
Mollusca — Gastropoda	43	14	4
Crustacea — Cirripedia	7	3	—
Crustacea — Isopoda and Amphipoda	2	3	—
Crustacea — Decapoda	12	12	5
Echinodermata — Asteroidea	5	1	—
Echinodermata — Ophiuroidea	1	—	—
Chordata — Ascidiacea	3	2	—
Totals	121	50	11

Parsons, K.E. and Ward, R.D., 1994. Electrophoretic and morphological examination of *Austrocochlea constricta* (Gastropoda : Trochidae): a species complex. *Australian Journal of Marine and Freshwater Research* 45: 1065–1085.

Phillips, A.W., 1975. The establishment of *Spartina* in the Tamar estuary, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 109: 65–75.

Pringle, A.W., 1982. Tidal immersion of the Tamar estuary *Spartina* marsh, Tasmania, Australia. *Papers and Proceedings of the Royal Society of Tasmania* 116: 143–152.

Pringle, A.W., 1993. *Spartina anglica* colonisation and physical effects in the Tamar estuary, Tasmania 1971–91. *Papers and Proceedings of the Royal Society of Tasmania* 127: 1–10.

Slack-Smith, S.M. and Brearley, A., 1987. *Musculista senhousia* (Benson, 1842); a mussel recently introduced into the Swan River estuary, Western Australia (Mollusca: Mytilidae). *Records of the Western Australian Museum* 13(2): 225–230.

Smith, B.J., 1995. *Tamar intertidal invertebrates: an atlas of the common species*. Queen Victoria Museum and Art Gallery: Launceston. 88 pp.

Thomson, J.M., 1959. The naturalization of the Pacific Oyster in Australia. *Australian Journal of Marine and Freshwater Research* 10: 144–149.

Wells, F.E., 1984. *A guide to the common molluscs of south-western Australian estuaries*. Western Australian Museum: Perth. 112 pp.

Willan, R.C., 1985. Successful establishment of the Asian mussel *Musculista senhousia* (Benson in Cantor, 1842) in New Zealand. *Records of the Auckland Institute Museum* 22: 85–96.

Appendix 1. List of intertidal invertebrate animals found on the Tamar Survey. The species listed here are those found south of George Town in the River Tamar. The distribution zones are as follows:

B = between George Town and the Batman Bridge; C = between the Batman Bridge; and Wndermere; D = South of Wndermere.

	ZONES
PORIFERA	
Identity unknown; about 3 spp.	B, C
CNIDARIA — ACTINARIA	
Actiniidae: <i>Anthopleura aureoradiata</i>	B
PLATYHELMINTHES —	
POLYCLADIDA	
Leptoplanidae: <i>Notoplana australis</i>	B
BRYOZOA	
Identity unknown; about 3 spp.	B, C
ANNELIDA — OLIGOCHAETA	
Tubificidae (possibly): identity unknown	-, -, D
ANNELIDA — POLYCHAETA	
(family identification tentative)	
Polynoidae: polynoid sp.	B
Phyllodocidae: phyllodocid sp.	B
Syllidae: syllid sp.	B
Nereidae: nereid spp.	B, C
Glyceridae: glycerid sp.	B
Eunicidae: eunicid spp.	B, C
Orbiniidae: orbiniid sp.	B
Spionidae: spionid sp.	B
Capitellidae: capitellid sp.	B
Maldanidae: maldanid sp.	B
Terebellidae: <i>Amphitrite rubra</i>	B
Terebellidae: terebellid sp.	B
Serpulidae: <i>Galeolaria caespitosa</i>	B
MOLLUSCA —	
POLYPLACOPHORA	
Ischnochitonidae: <i>Ischnochiton</i>	B
(<i>Ischnochiton</i>) <i>elongatus</i>	
— <i>Ischnochiton</i> (<i>Ischnochiton</i>) <i>variegatus</i>	B
Chitonidae: <i>Sypharochiton</i>	B, C
<i>pellisserpentis</i>	
Cryptoplacidae: <i>Cryptoplax striata</i>	B
Acanthochitonidae: <i>Acanthochitona granostrata</i>	B
— <i>Acanthochitona sueurii</i>	B
MOLLUSCA — BIVALVIA	
Arcidae: <i>Barbatia</i> (<i>Barbatia</i>) <i>pistachia</i>	B
— <i>Barbatia</i> (<i>Barbatia</i>) <i>squamosa</i>	B
Mytilidae: <i>Xenostrobus inconstans</i>	B, C, D
— <i>Xenostrobus pulex</i>	B
— <i>Musculista senhousia</i>	B, C
Pteriidae: <i>Electroma georgiana</i>	B
Ostreidae: <i>Crassostrea gigas</i>	B, C
Lasacidae: <i>Lasaea australis</i>	B
Mactridae: <i>Spisula</i> (<i>Notospisula</i>) <i>trigonella</i>	B
Mesodesmatidae: <i>Paphies</i> (<i>Atactodea</i>) <i>erycinaea</i>	B
Tellinidae: <i>Tellina</i> (<i>Macomona</i>) <i>deltoidalis</i>	B, C
Veneridae: <i>Katelysia peronii</i>	B, C
— <i>Katelysia scalarina</i>	B
— <i>Eumarcia fumigata</i>	B
— <i>Venerupis</i> (<i>Venerupis</i>) <i>anomala</i>	B
Hiattellidae: <i>Hiattella australis</i>	B
Teredinidae: <i>Bankia</i> spp.	B, C
Laternulidae: <i>Laternula tasmanica</i>	B
— <i>Laternula creccina</i>	B, C
Thraciidae: <i>Thraciopsis elongata</i>	B
MOLLUSCA — GASTROPODA	
Nacellidae: <i>Cellana tramoserica</i>	B
Acmaeidae: <i>Notoacmea flammea</i>	B, C
— <i>Notoacmea scabrillirata</i>	B
— <i>Notoacmea petterdi</i>	B, C
— <i>Collisella mixta</i>	B
Neritidae: <i>Nerita</i> (<i>Melanerita</i>) <i>atramentosa</i>	B
Fissurellidae: <i>Montfortula rugosa</i>	B
Turbinidae: <i>Astrarium</i> (<i>Micrastraea</i>) <i>aurea</i>	B
— <i>Turbo</i> (<i>Subninella</i>) <i>undulata</i>	B
Trochidae: <i>Monodonta</i> (<i>Austrocochlea</i>) <i>constricta</i>	B
— <i>Diloma</i> (<i>Fractarmilla</i>) <i>concamerata</i>	B, C
— <i>Diloma</i> (<i>Chlorodiloma</i>) <i>adelaidae</i>	B
— <i>Cantharidus</i> (<i>Phasianotrochus</i>) <i>irisodontes</i>	B
— <i>Echelus</i> (<i>Herpetopoma</i>) <i>aspersa</i>	B
— <i>Clanculus</i> (<i>Isocanculus</i>) <i>alloysii</i>	B
Cerithiidae: <i>Bittium granarum</i>	B, C
Batillariidae: <i>Batillaria</i> (<i>Zeacumantus</i>) <i>diemenensis</i>	B, C
— <i>Batillaria</i> (<i>Velacumantus</i>) <i>australis</i>	B, C
Campanilidae: <i>Campanile</i> (<i>Hypotrochus</i>) <i>monachus</i>	B
Littorinidae: <i>Littorina</i> (<i>Austrolittorina</i>) <i>unifasciata</i>	B
— <i>Bembicium melanostoma</i>	B, C
Hydrobiidae: <i>Tatea rufilabris</i>	B, C, D
— <i>Potamopyrgus antipodarum</i>	-, -, D
Assimineidae: <i>Assimineae</i> (<i>Metassimineae</i>) <i>buccinoides</i>	B, C, D
Hydrococcidae: <i>Hydrococcus brazieri</i>	B, C
Naticidae: <i>Polinices</i> (<i>Conuber</i>) <i>conicus</i>	B
Muricidae: <i>Bedevea paivae</i>	B
— <i>Lepsiella vinosa</i>	B

— <i>Thais orbita</i>	B	CRUSTACEA — DECAPODA	
Buccinidae: <i>Cominella lineolata</i>	B	Callianassidae: <i>Callianassa ceramica</i>	B, C
— <i>Nassarius (Niotha) pauperatus</i>	B, C	Palaemonidae: <i>Palaemon</i> sp.	B, C
— <i>Nassarius (Plicircularis) burchardi</i>	B	— <i>Palaemonetes</i> sp.	-, C, D
— <i>Nassarius (Zeuxis) pyrrhus</i>	B, C	— <i>Leander</i> sp.	B
— <i>Pleuroploca australasia</i>	B	Grapsidae: <i>Paragrapsus gaimardii</i>	B, C, D
Columbellidae: <i>Mitrella</i>	B	— <i>Paragrapsus quadridentatus</i>	B, C
(<i>Dentimitrella</i>) sp.		— <i>Cyclograpsus granulosus</i>	B, C
Conidae: <i>Conus (Floraconus)</i>	B	— <i>Helograpsus haswellianus</i>	B, C, D
<i>anemonae</i>		— <i>Brachynotus spinosus</i>	B, C
Philinidae: <i>Philine angasi</i>	B	Ocypodidae: <i>Macrophthalmus</i>	B, C, D
Pleurobranchidae: <i>Pleurobranchaea</i>	B	<i>latifrons</i>	
<i>maculata</i>		— <i>Heloecius cordiformis</i>	B, C
Dorididae: unknown sp.	B	Hymenosomatidae: <i>Amarinus laevis</i>	B, C, D
Onchidiidae: <i>Onchidella patelloides</i>	B	Mictyridae: <i>Mictyris platycheles</i>	B, C
Ellobiidae: <i>Ophicardelus ornatus</i>	B, C, D	ECHINODERMATA —	
Siphonariidae: <i>Siphonaria</i>	B	ASTEROIDEA	
(<i>Hubendickula</i>) <i>diemenensis</i>		Goniasteridae: <i>Tosia australis</i>	B
Amphibolidae: <i>Salinator fragilis</i>	B, C, D	Asterinidae: <i>Patiriella exigua</i>	B, C
CRUSTACEA — CIRRIPIEDIA		Asteriidae: <i>Allostichaster polyplax</i>	B
Iblidae: <i>Ibla quadrivalvis</i>	B	— <i>Uniophora granifera</i>	B
Balanidae: <i>Elminius covertus</i>	B, C	— <i>Coscinasterias calamaria</i>	B
— <i>Elminius modestus</i>	B, C	ECHINODERMATA —	
— <i>Balanus variegatus</i>	B, C	OPHIUROIDEA	
— <i>Epopella simplex</i>	B	Amphiuridae: <i>Ophiocentrus pilosus</i>	B
Chthamalidae: <i>Chthamalus</i>	B	CHORDATA — ASCIDIACEA	
<i>antennatus</i>		Identity unknown: about 3 spp.	B, C
Tetraclitidae: <i>Tetraclitella</i>	B		
<i>purpurascens</i>		(NOTE: Recently the gastropod <i>Austrocochlea</i>	
CRUSTACEA — ISOPODA &		<i>constricta</i> was split into three species (Parsons	
AMPHIPODA		and Ward, 1994). While it is probable that all	
Ligiidae: <i>Ligia australiensis</i>	B, C	three species are present in the Tamar, no	
Sphaeromatidae: <i>Sphaeroma</i>	-, C	attempt has been made to follow this study at	
<i>quoyanum</i>		present.)	
Talitridae: <i>Orchestia</i> sp.	B, C		

Appendix 2. Table showing the distribution of the common intertidal invertebrates of the Tamar.
For the position of the large squares see Map 2

Large Square Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
PLATYHELMINTHES																					
<i>Notoplana australis</i>	X		X		X	X		X													
ANNELIDA - POLYCHAETA																					
<i>Galeolaria caespitosa</i>	X		X	X	X	X															
MOLLUSCA - POLYPLACOPHORA																					
<i>Syph. pelisserpentis</i>	X	X	X	X	X	X	X	X	X	X	X		X								
MOLLUSCA - BIVALVIA																					
<i>Xeno. inconstans</i>	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X				
<i>Musc. senhousia</i>			X			X				X	X			X							
<i>Crassostrea gigas</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X						
<i>Lasaea australis</i>	X		X	X	X		X	X													
<i>Spis. (N.) trigonella</i>						X		X	X				X	X		X					
<i>Laternula spp.</i>	X	X	X		X		X	X													
MOLLUSCA - GASTROPODA																					
<i>Noto. flammea</i>	X		X	X	X	X			X												
<i>Nerita atramentosa</i>	X		X	X	X			X													
<i>Montfortula rugosa</i>	X			X																	
<i>Monodonta constricta</i>	X	X	X	X		X															
<i>Littorina unifasciata</i>	X			X	X		X														
<i>Bemb. melanostoma</i>	X	X	X	X		X	X	X	X	X	X	X	X	X	X						
<i>Tatea rufilabris</i>	X	X				X	X	X		X	X	X	X	X	X	X	X	X			
<i>Pot. antipodarum</i>																		X	X	X	X
<i>Ass. buccinoides</i>	X	X				X		X		X			X	X	X	X	X				
<i>Lepsiella vinosa</i>	X			X		X	X														
<i>Cominella lineolata</i>	X		X	X			X														
<i>Nass. pauperatus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X							
<i>Onch. patelloides</i>	X		X	X	X	X	X														
<i>Ophicardelus ornatus</i>	X	X		X	X	X	X	X	X	X	X	X			X	X					
<i>Siph. diemenensis</i>	X		X	X	X	X	X														
<i>Salinator fragilis</i>	X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X			
CRUSTACEA - CIRRIPIEDIA																					
<i>Elminius covertus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					
CRUSTACEA - DECAPODA																					
<i>Para. gaimardii</i>	X	X	X			X	X	X	X	X	X		X	X	X	X			X		
<i>Cyclo. granulatus</i>	X		X	X	X	X	X		X	X											
<i>Helo. haswellianus</i>	X	X				X	X	X	X	X				X	X	X					
<i>Macr. latifrons</i>	X	X	X		X			X			X		X	X	X	X					
<i>Heleo. cordiformis</i>	X	X	X		X		X	X	X	X			X								
<i>Amarinus laevis</i>						X							X	X	X	X	X	X			X
ECHINODERMATA - ASTEROIDEA																					
<i>Patirella exigua</i>	X		X	X	X	X	X		X												
TOTAL	29	16	23	20	19	24	21	19	15	15	12	9	13	13	13	10	5	4	3	1	2

PREDICTING SPECIES RICHNESS FOR AUSTRALASIAN FRESHWATER MACROINVERTEBRATES: DO WE WANT TO KNOW?

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Abstract

Grows, J.E. and Grows, I.O., 1997. Predicting species richness for Australasian freshwater macroinvertebrates: do we want to know? *Memoirs of the Museum of Victoria* 56(2): 483–490.

The identification of freshwater macroinvertebrates to family level is becoming increasingly popular for surveys, predictive models and pollution indices in Australia because it is quicker and cheaper than genus or species level identification, and it requires less specialised knowledge. Family richness has been used as a predictor of species richness for other taxonomic groups such as vertebrates, ants and plants and we were interested in seeing whether this might be a useful method for freshwater macroinvertebrates. Taxon lists from one Papua New Guinean and 34 Australian datasets from lentic and lotic waters were used to regress the number of families against the total number of taxa (species where possible). Also, the ability of the number of species and morphospecies within some orders (Coleoptera, Diptera, Ephemeroptera and Trichoptera) to predict overall species richness was investigated. The number of all families explained 91% of the variation in species richness. The number of species within each of the orders explained between 60 and 85% of the variation in overall species richness. We conclude that it would be possible to predict species richness in this way, particularly if sampling techniques and sampling effort were standardised. The terms 'species richness' and 'biodiversity' are often used synonymously although the former is only a subset of the latter. Some of the limitations and dangers of assessing species richness instead of biodiversity are discussed.

Introduction

Most freshwater studies addressing biodiversity have assumed that biodiversity and species richness are synonymous (e.g., Lang and Raymond, 1993; Allan and Flecker, 1993; but see Collier, 1993). Species richness is very expensive to determine using traditional methods and taxonomy. Rapid Biological Assessment (RBA) has been developed in order to overcome these difficulties. RBA is based on either the use of morphospecies rather than formally named species (basic RBA) or on identifying either subsets of communities or only identifying to taxonomic levels higher than species (ordinal RBA: Beattie et al., 1993). We present an evaluation of how effective ordinal RBA is likely to be for freshwater invertebrate communities.

Ordinal RBA assumes that higher-taxon richness or the number of species in taxonomic subsets are closely related to overall species richness but this has rarely been tested. Williams and Gaston (1994) used family richness to predict species richness of British ferns, British butterflies, Australian passerine birds and North and Central American bats. They found that for each of these groups of organisms, family richness explained at least 79% of the variation in species

richness and concluded that 'with careful choice of higher-taxon rank, it may be possible to re-deploy effort from taxonomically intensive to taxonomically extensive surveys'. Andersen (1995) used a similar approach to estimate species richness of Australian ants using generic diversity.

We obtained taxon lists from 34 datasets throughout Australia and one from Papua New Guinea and used family richness for the whole community and the numbers of morphospecies within four orders (Coleoptera, Diptera, Ephemeroptera and Trichoptera) as predictors of community species richness.

Methods

The number of families, total number of taxa and the numbers of coleopteran, ephemeropteran, trichopteran and dipteran taxa were determined for 34 taxon lists from surveys throughout Australia and 1 from Papua New Guinea (Table 1). The Australian studies were from all states and one territory: Western Australia, 10; New South Wales, 9; Victoria, 5; Queensland, 3; Northern Territory, 3; South Australia, 2; Tasmania, 2. The types of freshwater system were also very varied and eight of

Table 1. Details of the 35 datasets.

Dataset	Author(s)	Year	Area	State	Type
1	Bennison, Hillman and Suter	1989	Murray River and tributaries	NSW/SA	lowland river
2	Boulton	1988	Werribee River	VIC	intermittent
3	Boulton	1988	Lerderberg River	VIC	intermittent
4	Boulton and Lloyd	1991	Lower River Murray	SA	lowland river
5	Bunn, Edward and Loneragan	1986	Northern jarrah forest streams	WA	intermittent
6	Charlton (unpublished)	1994	Millstream Delta	WA	lowland river
7	Chessman and Growns, J.	1994	Williams River and tributaries	NSW	lotic
8	Chessman, McEvoy and Growns (unpublished)	1992	Upper Nepean River and tributaries?	NSW	lotic
9	Chessman, Growns, J., Hardwick and Holleley	1994	Warung Management Area	NSW	lotic
10	Chessman, Growns, J., Hardwick, Holleley, Jackson and McEvoy	1994	Dorrigo Management Area	NSW	lotic
11	Chessman, O'Connor and Holleley	1995	Tenterfield Management Area	NSW	lotic
12	Cosser	1988	Gowrie Creek*	QLD	lotic
13	Davis, Rosich, Bradley, Growns, J., Schmidt, and Cheal	1993	Perth wetlands*	WA	lentic
14	Davis, Barmuta and Balla	1988a	Serpentine River*	WA	lotic
15	Davis, Barmuta and Balla	1988b	Dirk Brook	WA	lotic
16	Davis, Harrington and Friend	1993	George Gill Range	NT	intermittent
17	De Deckker and Williams	1982	Tasmanian salt lakes	TAS	saline
18	Doeg	1984	Mitta Mitta River	VIC	lotic
19	Growns, I.	1992	Sutton catchment	WA	intermittent
20	Growns, I.	1992	Lewin catchment	WA	intermittent
21	Growns, I. and Davis	1994	Carey Brook	WA	lotic
22	Lake and Pearson (unpublished)	1988	Birthday Creek	QLD	lotic
23	Lake and Pearson (unpublished)	1988	Yuccabine Creek	QLD	lotic
24	Marchant	1982	Magela Creek	NT	lotic
25	Marchant, Mitchell and Norris	1984	Lower LaTrobe River and tributaries*	VIC	billabong lowland river
26	Metzeling, Graesser, Suter and Marchant	1984	Upper LaTrobe River and tributaries	VIC	lotic
27	Norris, Lake and Swain	1982	South Esk River*	TAS	lotic
28	Norris, Moore, Maher and Wensing	1993	Lake MacKenzie	NSW	lentic

Table 1 Continued

29	Norris, Moore, Maher and Wensing	1993	Lake Windamere	NSW	lentic
30	Outridge	1987	Magela Creek	NT	billabong
31	Pen and Potter (unpublished)	1990	Collie River*	WA	lotic
32	Robson (unpublished)	1990	Julimar Forest	WA	lotic
33	Towns	1985	Brown Hill Creek	SA	intermittent
34	Wright and Chessman (unpublished)	1992	Blue Mountains*	NSW	lotic
35	Yule	1995	Konaiano Creek	PNG	lotic

PNG = Papua New Guinea

*some sites polluted

the studies had at least some sites that were polluted (Table 1).

The total number of taxa for each study was taken as the number of recognised taxonomic units (RTUs) for that study, e.g., where chironomid larvae were not identified beyond family, this was counted as one RTU. Immature and unidentified taxa were not included unless they were the only RTU in that family or genus. Coleopteran adults and larvae were considered to be different RTU's unless they were both identified to the same published species name. Where identification was not taken even to family level, each group was taken as one RTU, e.g., Hydracarina.

Plots of the numbers of total taxa against the numbers of families and coleopteran, dipteran, ephemeropteran and trichopteran taxa were examined for outliers. The state in which each study occurred was superimposed on the plot of numbers of families, in order to look for any regional variation.

Linear regression was used to examine the relationships between the total numbers of taxa and the numbers of families and the numbers of coleopteran, ephemeropteran, trichopteran and dipteran taxa. All data were $\log_{10}(x+1)$ transformed and residuals were examined for normality using Normal Scores plots.

To test the predictive value of the regression of number of families versus total numbers of taxa, data on numbers of families and species for single sites were used from Marchant et al. (1995). The data from the lower La Trobe and Thomson Rivers and the upper La Trobe River were not used for this test as they had been used

in the calculation of the regression equation. Percentage error in prediction of species richness was calculated by subtracting the number of predicted species from the actual number of species, so that a negative error means that more species were predicted than were actually recorded. Percentage error was plotted against number of families to identify any systematic errors.

Results

All regressions were highly significant. The number of families explained 91% of the variation in the number of total taxa (Table 2). The number of taxa from the taxonomic sub-groups were poorer predictors of total numbers of taxa with the numbers of coleopteran taxa giving the best result (Table 2).

For most states, not enough datasets were available to assess regional variation. However, the plot suggested that, for the datasets available, lotic systems in south-west Western Australia had low species richness, whereas those in NSW had consistently high species richness (Fig. 1). There was no evidence that the different states showed different relationships between species and family richness, i.e. the intercepts and slopes of the lines for each state appeared very similar (Table 2).

The plot of total number of taxa against the number of coleopteran taxa (Fig. 2a) showed that Carey Brook (study 21) and the Serpentine River (14) had lower proportions of beetle taxa than would have been expected and the Collier River (31) had a higher proportion than would

Table 2. Regression results of predictions of total numbers of taxa using $\log(x+1)$ transformed data.

Independent variable	n	Intercept	Slope	r ²
Number of families:				
All datasets	35	-0.488	1.530	0.91
NSW	9	-0.730	1.671	0.98
VIC	6	0.062	1.298	0.80
WA	10	-0.046	1.260	0.83
Number of coleopteran taxa	35	1.174	0.713	0.85
Number of dipteran taxa	35	0.981	0.732	0.70
Number of trichopteran taxa	35	1.356	0.606	0.68
Number of ephemeropteran taxa	35	1.573	0.632	0.60

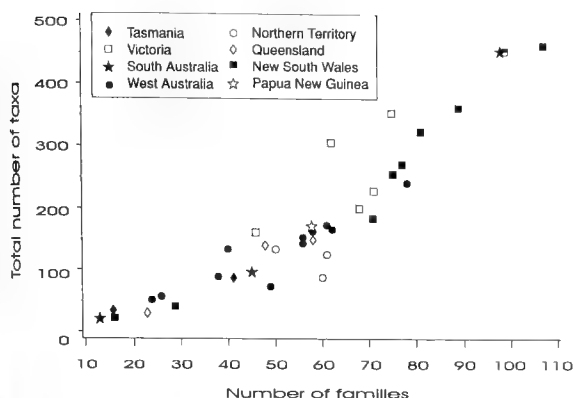


Figure 1. Plot of total number of taxa against number of families for the 35 studies. The state in which the study was done is overlaid.

have been expected. All these 3 areas are in south-west Western Australia. The same plot for dipteran taxa (Figure 2b) showed that Carey Brook had a high proportion of Diptera whereas the Werribee (study 2) and Lerderderg rivers (study 3), which are both ephemeral rivers in Victoria, had low proportions of dipteran

larvae. This plot also showed a marked difference in the proportions of Diptera between the Williams River (study 7) and the River Murray and tributaries (study 1), although they both had similar total numbers of taxa. The plot for Ephemeroptera (Figure 2c) indicated that the River Murray and tributaries, the Perth wetlands (study 13) and the Werribee and Lerderderg Rivers had low numbers compared to their total numbers of taxa. The trichopteran plot (Figure 2d) indicated that the River Murray and tributaries had low numbers of caddis whereas the Werribee and Lerderderg Rivers had high numbers compared to their total numbers of taxa.

The prediction of species richness from family richness for 19 single sites (data from Marchant et al., 1995) gave a mean error of -7.7% (standard error, 2.5) with a maximum error of -31% . The plot of percent error against number of families showed that roughly half of the sites were predicted to within 10% of the actual species richness (Fig. 3). Also, 14 out of the 19 predictions were for more species than actually occurred.

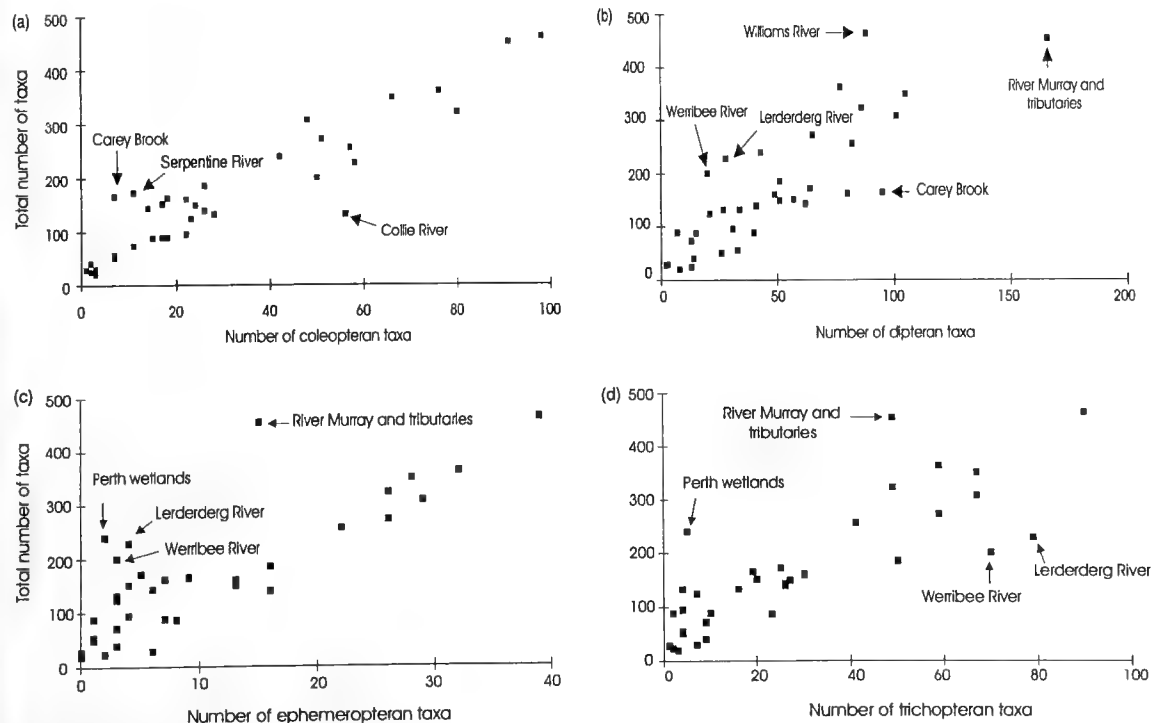


Figure 2. Plots of total number of taxa against numbers of taxa for (a) Coleoptera, (b) Diptera, (c) Ephemeroptera and (d) Trichoptera.

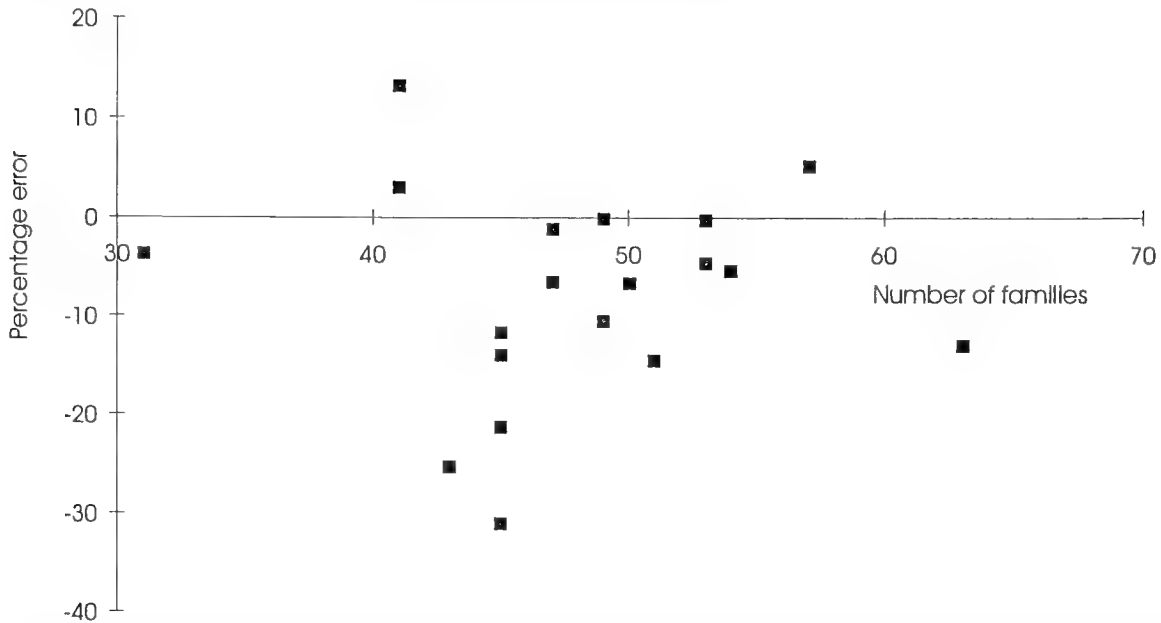


Figure 3. Plot of percentage error in prediction of species richness against number of families for the 19 single sites from Marchant et al. (1995).

Discussion

The number of families was a very good predictor of community species richness (i.e., total number of taxa) whereas the taxon richness for the four orders were not such good predictors; beetles were the best of the four. This suggests that analysing whole communities to coarse taxonomic levels may be more reliable than species level identification of indicator groups, if estimates of whole community species richness are wanted.

There was no evidence that there were different relationships between numbers of families and community species richness in different regions of Australia. However, there was some evidence that lotic systems in NSW had very high species richness whereas lotic systems in south-west Western Australia had low species richness. Bunn and Davies (1990) suggested that the low species richness of south-west Western Australian lotic systems may be due to the area's isolation, historical aridity and low primary productivity. Although low in numbers of species for many groups, this area has a very high proportion of endemics among its flora and fauna, including the lotic macroinvertebrates (CSIRO, 1992; Christensen, 1992). In contrast, high levels of species richness have previously been

observed for tabanid diptera and odonates, as well as for other communities, on the north coast of NSW, which has been designated the Macpherson-Macleay overlap (CSIRO, 1991). MacArthur (1972) observed that lotic invertebrates are the principal exception to the rule that the tropics have greater biodiversity than temperate areas. However, Lake et al. (1994) found that two Queensland creeks had significantly higher species richness than streams of similar stream orders in Victoria. Our data did not show higher species richness for tropical areas but this may be due to the small number of datasets from the tropics in this study.

Several of the species lists showed that where communities are low in species numbers of one taxonomic group, they are high for another group. The intermittent Werribee and Lerderg Rivers in Victoria had low numbers of dipteran larvae and mayfly nymphs but high numbers of caddis fly larvae. Carey Brook, a in south-west Western Australia, had low numbers of beetles but high numbers of dipteran larvae. There are doubtless historical and evolutionary reasons for these patterns but it is interesting to note that the overall relationship between numbers of families and community species richness was the same for these areas as for all the other studies.

The predictions of species richness for single sites were not good. Only about half of the predictions for single sites fell within 10% of the actual species richness and errors of up to 31% occurred. The majority of the predictions for single sites were for higher numbers of species than actually occurred. This may in part be because Marchant et al. (1995) included oligochaetes, triclads and mites as single taxa. However, several of the 35 studies used to calculate the regression equation also did this. The consistently high predicted species numbers are more likely to be because the predictions are for single sites whereas the regression was of studies of multiple sites in an area. The lower sampling effort for the single sites would be expected to obtain a lower proportion of species within each family compared to multiple site studies. For example, at most sites you would be likely to find beetles from the family Dytiscidae. However, there are likely to be different species of dytiscids at different sites. So a survey of several sites would find more species of dytiscids than a survey of only one site, whereas both surveys would record only one family for the different numbers of species. This highlights the care with which this type of predictive technique must be used.

Our results should be treated with some caution as the sampling intensity, methods and taxonomy varied among studies and the geographic distribution of the studies was uneven. However, we believe that we have shown that this approach would be highly successful in predicting the species richness of freshwater macroinvertebrates for an area. It might also show interesting patterns, such as the apparent high levels of species richness in northern NSW. In addition, our observation that where one group of organisms in a community has low species richness, another taxonomic group in the same community may have high species richness, has interesting evolutionary implications.

However, we are concerned that the almost exclusive focus on species richness in biodiversity assessment is unwarranted. Biodiversity is a difficult concept to define as it comprises many different ideas, of which species richness is only one. We need to know what the species are: an assessment of their endemism, rarity, susceptibility to extinction and distribution can then be made, or at least attempted. It is also important to know where they fit into their community, i.e. whether they are needed for the continuing survival of other organisms, and whether they are an example of a scientifically important

phenomenon, such as evolution (see Richardson, this volume). It is obviously impossible for all of this information to be obtained for all species, let alone in the time frames required by managers and legislators. However, this does not mean that species richness alone should be used as a surrogate for biodiversity. Scientists need to reach a consensus on what aspects of biodiversity need to be considered for conservation purposes and then communicate this to the wider community.

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References

- Allan, J.D and Flecker, A.S., 1993. Biodiversity conservation in running waters. *Bioscience* 43: 32-43.
- Anderson, A.A., 1995. Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biological Conservation* 73: 39-43.
- Beattie, A.J., Majer, J.D. and Oliver, I., 1993. Pp. 4-14 in: *Rapid biodiversity assessment: a review*. Proceedings of the Biodiversity Assessment Workshop, Macquarie University.
- Bennison, G.L., Hillman, T.J. and Suter, P.J., 1989. *Macroinvertebrates of the River Murray (survey and monitoring: 1980-1985)*. Murray Darling Basin Commission: Canberra.
- Boulton, A.J., 1988. *Composition and dynamics of macroinvertebrate communities in two intermittent streams*. Ph.D. thesis, Monash University.
- Boulton, A.J. and Lloyd, L.N., 1991. Macroinvertebrate assemblages in floodplain habitats of the lower River Murray, South Australia. *Regulated Rivers: Research and Management* 6: 183-201.
- Bunn, S.E. and Davies, P.M., 1990. Why is the stream fauna of south-western Australia so impoverished? *Hydrobiologia* 194: 169-176.
- Bunn, S.E., Edward, D.H. and Loneragan, N.R., 1986. Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: community structure. *Freshwater Biology* 16: 67-91.
- Chessman, B.C. and Growns, J.E., 1994. *Williams River aquatic macroinvertebrate study*. Australian Water Technologies, EnSight Report no. 94/84.
- Chessman, B.C., Growns, J.E., Hardwick, R. and Holleley, D., 1994. *Warung Forest Management*

- Area: aquatic fauna report*. Australian Water Technologies, EnSight Report no. 94/187.
- Chessman, B.C., Growns, J.E., Hardwick, R., Holleley, D., Jackson, J.E. and McEvoy, P.K., 1994. *Dorrigo three-year environmental impact statement area: aquatic fauna report*. Australian Water Technologies, Science and Environment Report no. 93/123.
- Chessman, B.C., O'Connor, R. and Holleley, D., 1995. *Tenterfield Forest Management Area: aquatic environment report*. Australian Water Technologies, EnSight Report no. 95/32.
- Christensen, P.E.S., 1992. *The Karri Forest. Its conservation significance and management*. CALM, Western Australia.
- Collier, K., 1993. Review of the status, distribution, and conservation of freshwater invertebrates in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27: 339–356.
- Cosser, P.R., 1988. Macroinvertebrate community structure and chemistry of an organically polluted creek in south-east Queensland. *Australian Journal of Marine and Freshwater Research* 39: 671–683.
- CSIRO, 1991. *The insects of Australia*. Melbourne University Press: Melbourne.
- Davis, J.A., Barmuta, L.A. and Balla, S.A., 1988a. *Serpentine River and Gooralong Brook aquatic fauna study*. Murdoch University, WA.
- Davis, J.A., Barmuta, L.A. and Balla, S.A., 1988b. *Dirk Brook aquatic fauna study*. Murdoch University, WA.
- Davis, J.A., Harrington, S.A. and Friend, J.A., 1993. Invertebrate communities of relict streams in the arid zone: the George Gill Range, Central Australia. *Australian Journal of Marine and Freshwater Research* 44: 483–505.
- Davis, J.A., Rosich, R.S., Bradley, J.S., Growns, J.E., Schmidt, L.G. and Cheal, F., 1993. *Wetlands of the Swan coastal plain. Volume 6. Wetland classification on the basis of water quality and invertebrate community data*. Water Authority of Western Australia/Environmental Protection Authority of Western Australia.
- De Deckker, P. and Williams, W.D., 1982. Chemical and biological features of Tasmanian salt lakes. *Australian Journal of Marine and Freshwater Research* 33: 1127–1132.
- Docg, T., 1984. Response of the macroinvertebrate fauna of the Mitta Mitta River, Victoria, to the construction and operation of Dartmouth Dam. 2. Irrigation release. *Occasional Papers from the Museum of Victoria* 1: 101–108.
- Growns, I.O., 1992. *Macroinvertebrate community structure in the streams of the southern forests of Western Australia: the influence of seasonality, longitudinal gradients and forestry activities*. Ph. D. thesis, Murdoch University.
- Growns, I.O. and Davis, J.A., 1994. Longitudinal changes in near-bed flows and macroinvertebrate communities in a Western Australian stream. *Journal of the North American Benthological Society* 13: 417–438.
- Lake, P.S., Schreiber, E.S.G., Milne, B.J. and Pearson, R.G., 1994. Species richness in streams: patterns over time, with stream size and with latitude. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 24: 1822–1826.
- MacArthur, R.H., 1972. *Geographical ecology*. Harper and Row: New York.
- Marchant, R., 1982. Seasonal variation in the macroinvertebrate fauna of billabongs along Magela Creek, Northern Territory. *Australian Journal of Marine and Freshwater Research* 33: 329–42.
- Marchant, R., Barmuta, L.A. and Chessman, B.C., 1995. Influence of sample quantification and taxonomic resolution on the ordination of macroinvertebrate communities from running waters in Victoria, Australia. *Marine and Freshwater Research* 46: 501–506.
- Marchant, R., Mitchell, P. and Norris, R., 1984. A distribution list for the aquatic invertebrates in the lowland region of the LaTrobe River, Victoria. *Occasional Papers from the Museum of Victoria* 1: 63–79.
- Metzeling, L., Graesser, A., Suter, P. and Marchant, R., 1984. The distribution of aquatic macroinvertebrates in the upper catchment of the La Trobe River, Victoria. *Occasional Papers from the Museum of Victoria* 1: 1–62.
- Norris, R.H., Lake, P.S. and Swain, R., 1982. Ecological effects of mine effluents on the South Esk River, north-eastern Tasmania III. Benthic macroinvertebrates. *Australian Journal of Marine and Freshwater Research* 33: 789–809.
- Norris, R.H., Moore, J.L., Maher, W.A. and Wensing, L., 1993. Limnological characteristics of two coastal dune lakes, Jervis Bay, south eastern Australia. *Australian Journal of Marine and Freshwater Research* 44: 437–458.
- Outridge, P.M., 1987. Possible causes of high species diversity in tropical Australian freshwater macrobenthic communities. *Hydrobiologia* 150: 95–107.
- Richardson, A.M.M., Swain, R. and Wong, V.E., 1996. The crustacean and molluscan fauna of Tasmanian saltmarshes: conservation of a transitional habitat. *Memoirs of the Museum of Victoria* 56.
- Towns, D.R., 1985. Limnological characteristics of a South Australian intermittent stream, Brown Hill Creek. *Australian Journal of Marine and Freshwater Research* 36: 821–837.
- Williams, P.H. and Gaston, K.J., 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation* 67: 211–217.
- Yule, C.M., 1995. Benthic invertebrate fauna of an aseasonal tropical mountain stream on Bougainville Island, Papua New Guinea. *Marine and Freshwater Research* 46: 507–518.

CONSERVATION OF AQUATIC INVERTEBRATE COMMUNITIES IN CENTRAL AUSTRALIA

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Abstract

Davis, J., 1997. Conservation of aquatic invertebrate communities in central Australia. *Memoirs of the Museum of Victoria* 56(2): 491-503.

Central Australian waterbodies are an important focus for both nature conservation and tourism within the arid zone. Recent sampling of the West MacDonnell Ranges in 1993 and 1994, and the George Gill Range, in 1986, revealed the presence of 'relict streams' containing elements of an invertebrate fauna, and possibly flora, that have persisted since the last 'wet' phase in central Australia. These streams appear to be sustained by localised regions of permanently discharging groundwater and the effects of past landuses, including aboriginal useage and cattle grazing, do not appear to have been major or irreversible. However, the popularity of ecotourism in the region is rapidly increasing and appropriate management is needed to ensure that these important aquatic habitats are not lost or degraded through over-utilisation of the groundwater resource.

Introduction

The ranges of central Australia, including the MacDonnells, James, Krichauff and George Gill Ranges, are dominant landscape features within the region and the gorges of the West MacDonnell and George Gill Ranges are very popular tourist destinations. The ranges lie within one of the driest regions of Australia and the climate is characterised by extreme diel and seasonal temperature differences. The average rainfall is 250 mm per annum and, although summer rain is dominant, rainfall variability is high. Annual total evaporation is in the order of 3200 mm. Aspects of the physical and biological characteristics of the area are described by Gibson and Cole (1993), Latz et al. (1981), Thompson (1991) and Van Oosterzee (1991).

The extreme aridity of the region has resulted in the common perception that it contains few waterbodies. Although large volumes of permanent surface water are not present, the central Ranges contain a wide variety of aquatic habitats, ranging from permanent groundwater fed seeps and springs to deep gorges, permanent and semi-permanent river pools, shallow river wetlands, temporary and ephemeral rock pools and claypans. The only waterbodies not represented are permanently flowing streams and rivers.

The aridity of the region and the belief (amongst limnologists, at least) that little surface water is present, have undoubtedly been the reasons as to why so little has been known of the aquatic ecosystems within the central Ranges. The Horn Scientific Expedition of 1894 was the

first major scientific study of the ranges and remains one of the few publications on the aquatic invertebrate fauna of the region. The records of fishes and aquatic invertebrates published as part of the report of the expedition (Spencer, 1896) are now of considerable value because they provide an indication of species present in central Australia at the onset of European settlement. Keast (1959) briefly mentioned dragonflies, freshwater snails and fish in a discussion of the relict animals and plants of the MacDonnell Ranges, and Williams and Siebert (1963) noted the presence of some species of snails, microcrustaceans and insects in their paper on the chemical composition of central Australian waterbodies. Davis et al. (1993) described the aquatic invertebrate fauna of the George Gill Range and a small number of sites in the West MacDonnell Ranges (some 200 km to the southwest). The fishes of the region have been more extensively studied than the invertebrate fauna although much of this work exists as unpublished reports or as collections in museums. Published accounts include Glover and Sim (1978), Glover (1982), Larson and Martin (1989), Crowley and Ivantsoff (1990) and Kodric-Brown and Brown (1993). Recently, Gibson and Cole (1993) provided a list of species of fish known from some of the permanent waterbodies within the West MacDonnells.

Davis et al. (1993), in their work on the aquatic systems of the George Gill Range noted that a small proportion of the fauna appeared to

be a relictual stream fauna. In particular, the presence of an obligate stream invertebrate, the waterpenny, *Sclerocyphon fuscus*, was of interest because it was unlikely to be capable of dispersal across the large tracts of arid land that now separate the George Gill Range from southern Australia where it is also found.

The objectives of this study were to extend the work of Davis et al. (1993) to describe the invertebrate fauna of the waterbodies of the West MacDonnell Ranges and to determine the extent of the distribution of the waterpenny, and relictual stream habitats, in central Australia.

Methods

Physico-chemical variables and the aquatic invertebrate and fish fauna of waterbodies in the West MacDonnell Ranges were sampled in September 1993 and over the period February to April, 1994. The locations of sampling sites are listed in Table 1 and illustrated in Fig. 1. The majority of the waterbodies studied occurred within the headwaters of tributaries of the Finke River, including Ellery Creek and the Hugh River. Data from an earlier study of the George Gill Range was also included to enable a wider comparison of aquatic invertebrate communities within central Australia.

Conductivity and pH were recorded at all sites. Semi-quantitative and qualitative collection methods were used to sample as wide a

range of aquatic microhabitats as possible. Many sites could only be reached on foot which limited the amount, and type, of collecting apparatus that could be used. In the larger waterbodies six replicate samples were collected by sweeping a long handled net (250 micron mesh) through the water column and against the substrate, in a yo-yoing motion, over a distance of 10 m. In the smaller stream sites kick samples were collected by disturbing the sediments at the front of the net. Invertebrates were also hand-picked with forceps from individual rocks and wood. Expandable mesh traps, baited with chicken pellets, were set overnight at the larger waterbodies to catch yabbies.

Although some samples were sorted in the field most were preserved in 100% alcohol and returned to the laboratory for sorting and identification. Identified material is currently stored, in 70% ethanol, in the School of Biological and Environmental Sciences at Murdoch University.

Fish were sampled in the larger waterbodies using a 1mm mesh seine net dragged over a distance of approximately 25 m. In smaller waterbodies fish were caught with a long handled net. All fish were identified in the field and returned to the water with the exception of a small number of representative specimens. These were preserved in 100% alcohol and stored for subsequent confirmation of identification in the laboratory.

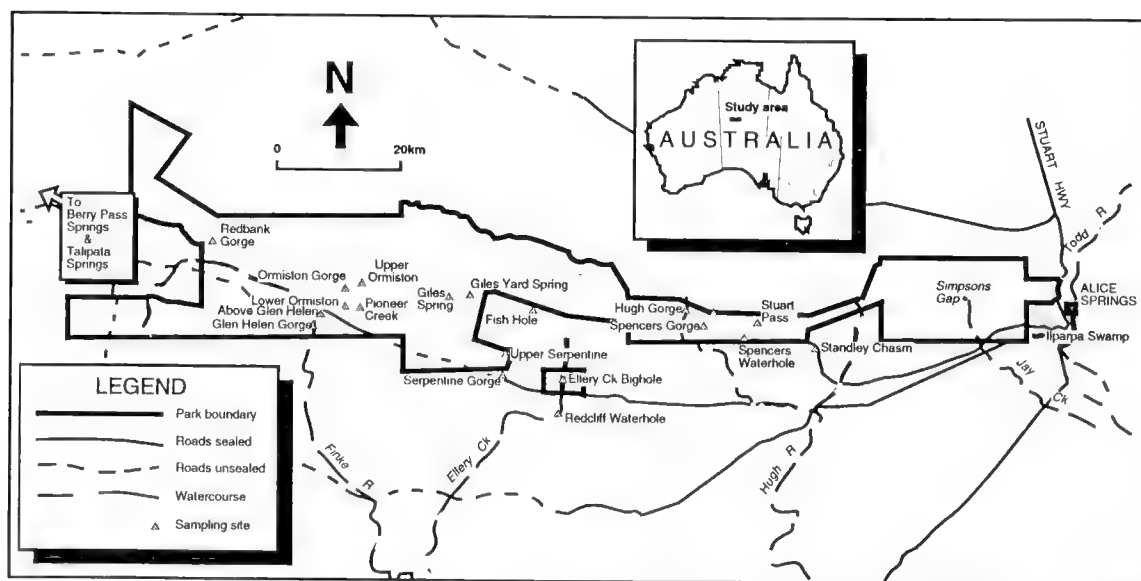


Figure 1. Location of waterbodies sampled in the West MacDonnell Ranges, Northern Territory.

Table 1. Names, codes, conductivity, pH and presence of fishes and waterpennies (denoted by *) for sites sampled in the West MacDonnell Ranges and other localities within the Central Ranges, Northern Territory.

Sites	Code	Conductivity uS/cm	pH	Presence of fish	Presence of waterpenny <i>Sclerocyphon</i> <i>fuscus</i>
West MacDonnell Ranges					
Redbank Gorge	REDB	190	7.1	*	
Upper Redbank Gorge	URED	190	7.1		
Pioneer Creek	PION	12 800	7.8	*	
Waterhole above Glen Helen	ABGH	8 140	7.8	*	
Glen Helen Gorge	GHG	2 330	7.8	*	
Ormiston Gorge	ORMG	160	7.4	*	
Pool above Ormiston Gorge	UORM	160	7.4		
Pool below Ormiston Gorge	ORMP	160	7.4		
Serpentine Gorge	SERP	134	7	*	
Upper Serpentine Gorge	USER	71	6.6		*
Ellery Creek Big Hole	ECBH	242	6.8	*	
Redcliff Waterhole	REDC	462	7.8	*	
Giles Yard Spring	GYS	27	5.8		*
Giles Spring	GS	53	4.8		*
Hugh Gorge		193	8		*
Spencers Gorge	SPEN	NA	NA	*	
Spencers Waterhole	SPW	440	7.8	*	
Stuart's Pass		400	8	*	
Fishhole on Ellery Ck		338	7.6	*	
Talipata Springs	TALI	80	8.2		*
Berry Pass	BERR	NA	NA		
Ilparpa Swamp	ILP	NA	NA		
East MacDonnell Ranges					
Emily Gap		300	7.7	NA	
John Hayes Rockhole		119	7.4	*	
Trephina Gorge	TRE	855	7.78	NA	
Glen Annie Gorge		690	9.5	NA	
Krichauff and James Ranges					
Kanara Ck (Oasis Ck)		1 400	8.76	*	
West Palm Paddock Spring		1 142	8.4	*	
Finke Gorge Pool 1		NA	NA	*	
Little Palm Ck		393	7.8	*	
Finke Gorge Pool 2		1 624	8	*	

Table 1 continued

Boggy Hole	BH	1 190	7.6	*	
Running Waters		1 880	8.2	*	
Illamurta Spring		NA	NA		
Illara Waterhole		1 830	7.5	*	
George Gill Range					
Kings Canyon	KC	27	5.7		
Penny Springs	PS	99	6.7		*
Tjindri Tjindri	TT	76	6.6		
Reedy Rockhole	RR	362	6.3		
Wanga Ck	WC	NA	NA		
Kathleen Springs	KS	540	6.8		
Stokes Ck	SC	73	6.3		*

A site by species matrix was constructed using an Excel spreadsheet. Multivariate analyses were performed using the cluster and ordination techniques available from the PRIMER software package of Clarke and Warwick (1994).

Results

Physicochemistry

The waterbodies of the West MacDonnell Ranges display a wide range of salinities (Table 1). The freshest sites were Giles Yard Spring (27 $\mu\text{S}/\text{cm}$), Upper Serpentine Gorge (71 $\mu\text{S}/\text{cm}$) and Talipata Springs (80 $\mu\text{S}/\text{cm}$). Pioneer Creek (a pool adjacent to a small mound spring) was the most saline waterbody sampled, with a conductivity of 12,800 $\mu\text{S}/\text{cm}$. Conductivities were also high at waterbodies downstream of Pioneer Creek, with a conductivity of 8,140 $\mu\text{S}/\text{cm}$ recorded at the waterhole above Glen Helen, and 2,330 $\mu\text{S}/\text{cm}$ recorded at Glen Helen Gorge.

Many sites were circumneutral (Table 1) with respect to pH. Giles Spring was the most acidic site with a pH of 4.8 while Talipata Springs was the most alkaline at 8.2. The highest pH recorded from all waterbodies sampled within the region was 9.5 at Glen Annie Gorge at the eastern end of the East MacDonnell Ranges. The lowest pH was 5.7 recorded at the Garden of Eden in Kings Canyon, in the George Gill Range.

Aquatic invertebrate fauna

Although a total of 36 sites were sampled in the West MacDonnell Ranges, East MacDonnell Ranges and Krichauff Range (Palm Valley) during the period September 1993 to April 1994,

only the fauna from 20 sites (18 West MacDonnell sites plus Boggy Hole and Trephina Gorge) were processed and analysed within the resources available for the project. The 20 sites for which entire macroinvertebrate community data are available are indicated by the presence of a code in Table 1. The presence or absence of taxa at the 20 sites is given in Table 2. The presence or absence of the waterpenny, *Sclerocyphon fuscus*, and the presence or absence of fish, were noted for all sites (Table 1) because this information could be determined directly in the field.

A total of 75 macroinvertebrate taxa was recorded from the West MacDonnell Ranges (Table 2). Although this total represents the majority of species present it remains an underestimate of the entire fauna for several reasons. Greater sampling effort, for example, at seasonal or monthly intervals and at additional sites, will undoubtedly increase this total. Additional species will be added when further groups, including the Oligochaeta, Hydracarina, Chironomidae and microcrustacea are fully identified to the level of species.

Ormiston Gorge (26 taxa), Ellery Creek Big Hole (23 taxa) and Boggy Hole (22 taxa) were the most species-rich sites while Pioneer Creek (4 taxa) and Trephina Gorge (4 taxa) were the most depauperate. A total of 19 species recorded in the West MacDonnell Ranges did not occur in the George Gill Range. These include the gastropods *Austropeplea lessoni* and *Thiara* sp., the freshwater prawn, *Macrobrachium* sp., the damselflies, *Austrolestes aridus* and *Caliagrion billinghami*, the dragonflies, *Aeshna brevistyla* and *Notolibullela bicolor*, the water strider,

Table 2. Presence/absence of taxa recorded at waterbodies in the West MacDonnell Ranges and other sites within the Central Ranges region, NT. A key to site codes is given in Table 1.

[illegible]

Table 2. continued

	TALI	BERR	UPED	REDB	UCRM	ORMG	ORMP	PION	ABHG	GHG	GYS	USER	SEPP	ECBH	REDC	SPEG	SPW	BH	ILP	TRE
<i>Microvelia</i> sp.																				
<i>Mesovelia</i> sp.																				
<i>Enithares</i> sp.																				
<i>Anisops occipitalis</i>																				
<i>Micronecta</i> nr <i>annae</i>																				
<i>Agriaptocorixa euryzona</i>																				
Nepidae																				
<i>Necterosoma penicillatum</i>																				
<i>Necterosoma regulare</i>																				
<i>Necterosoma</i> sp. (larva)																				
<i>Sternopriscus multimaculatus</i>																				
<i>Hyphydrus elegans</i>																				
<i>Sandracottus bakewellii</i>																				
<i>Eretes australis</i>																				
<i>Cybisiter tripunctatus</i>																				
<i>Macrogyrus gouldi</i> ?																				
<i>Hydrochus</i> sp. 1																				
<i>Hydrochus</i> sp. 2																				
<i>Berosus</i> sp.																				
Hydrophilidae sp. (larva)																				
Hydrophilidae sp. (adult)																				
<i>Hydraena</i> sp.																				
<i>Sclerocyphon fuscus</i>																				
Chironomidae																				
<i>Dicrolentipes</i> nr <i>taylori</i>																				
Ceratopogonidae																				
Culicidae																				
<i>Simulium ornaticipes</i>																				
Tabanidae																				
Stratiomyidae																				
Ephydriidae																				
Psychodidae ?																				
<i>Heliothira simplex</i>																				
<i>Enomus continentalis</i>																				
<i>Oecetis</i> sp. A																				
<i>Oecetis</i> sp. B																				
<i>Triplectides australis</i>																				
<i>Triplectides volda</i>																				
Total number of taxa	15	10	6	15	14	26	8	4	12	16	17	4	17	23	10	9	7	22	10	5

Gerridae, the caddisfly, *Triplectides volda*, and the beetles, *Necterosoma regulare*, *Sternopriscus multimaculatus*, *Eretes australis*, *Cybister tripunctatus* and *Berosus* sp. A further 18 species recorded in the George Gill Range have not been recorded from the West MacDonnells. These include the pea clam, *Pisidium*, the dragonfly, *Trapezostigma stenoloba*, the dipteran, Thaumaleidae, and numerous beetles.

The Insecta were more diverse, in terms of species richness, than the Crustacea, which probably reflects the predominantly fresh nature of these waterbodies. Similar to results recorded previously for the George Gill Range no Amphipoda, Isopoda or Plecoptera were recorded in the West MacDonnell Ranges.

The Odonata (dragonflies and damselflies) and the Coleoptera (beetles) were the most diverse groups of insects present, both being represented by 16 taxa. The Odonata are perhaps the most spectacular invertebrates associated with aquatic systems in central Australia. The most common species were *Diplacodes haematodes* and *Orthetrum caledonicum*. Distributional records (Watson 1974; Watson et al. 1991) indicate that these species and others, including *Austrogrion watsoni*, *Ischnura aurora*, *Xanthagrion erythroneurum*, *Diplacodes bipunctata*, *Hemicordulia tau*, *Hemicordulia watsoni*, and *Aeshna brevistyla*, are widespread throughout Australia. *Caliagrion billinghursti* has previously been recorded from Victoria, coastal NSW and southern coastal Queensland. *Orthetrum migratum* also occurs in coastal Queensland and northern Australia. *Trapezostigma stenoloba* which has a similar distribution to *Orthetrum migratum* and occurs in the George Gill Range, was not recorded in the West MacDonnells. *Austrogomphus gordonii* has only previously been recorded from the Pilbara region of WA and from the George Gill Range. *Notolibellula bicolor* which was only recorded from Giles Yard Spring and Talipata Springs, has also been recorded from the northern NT and the Kimberley region of WA. *Hemicordulia flava* appears to be endemic to the Central Ranges region.

Several species of Coleoptera displayed specific environmental preferences. The waterpenny, *Sclerocyphon fuscus* which displays a disjunct distribution occurring in the George Gill Range, South Australia and western Victoria, was restricted to the relict stream habitats. To date it has been recorded from Giles Yard Spring, Giles Spring (sampled in 1986), Talipata Springs, Upper Serpentine Gorge, upper Hugh

Gorge and Penny Springs and upper Stokes Creek in the George Gill Range. Additional records of the waterpenny at Talipata Gorge and Bowmans Gap were provided by David Albrecht and Terry Mahney, respectively. The large diving beetle, *Sandracottus bakewelli*, which has been recorded from Upper Redbank Gorge, Talipata Springs, upper Hugh Gorge and the George Gill Range appears to only occur in waterbodies where fish are absent. A similar distribution has also been recorded for the large backswimmer *Enithares* sp. In contrast to the restricted distributions of *Sclerocyphon* and *Sandracottus*, the small dytiscid, *Necterosoma regulare*, appeared to be a highly tolerant species, being widespread and the only organism recorded in large numbers in the most saline waterbody, Pioneer Creek.

Although the Chironomidae, as a family, are diverse and widespread, occurring within almost all aquatic habitats in the West MacDonnell Ranges, one species, *Dicrotendipes nr taylora*, appeared to be restricted to Giles Yard Spring and Talipata Springs. Within these habitats it was both abundant and conspicuous on the upper surfaces of the rocky substrate, where it occurred within cases constructed from sediment and algae.

Fishes

Eleven species of fish have been recorded from the waterbodies of the West MacDonnell Ranges (Davis, in press). Eight species were recorded from central Australia by the Horn Expedition (Zietz, 1896), of which five were new. With the exception of one species, *Nematocentris winnecki*, which is a synonym of *Melanotaenia splendida tatei* (the desert rainbowfish) all species are still present within central Australia. Fish were not recorded from Upper Redbank Gorge, Upper Serpentine Gorge, Hugh Gorge, Giles Yard Spring, Giles Spring, Talipata Springs, Berry Pass Springs, nor any sites in the George Gill Range.

Introduced fish are generally absent from central Australia with the exception of the mosquitofish, *Gambusia affinis*, recorded from John Hayes Rockhole and the swordtail, *Xiphophorus helleri*, recorded in a dam near Pine Gap (both of which are isolated from the Finke drainage system).

Multivariate analyses

The dendrogram produced by the PRIMER program CLUSTER from the presence/absence macroinvertebrate data for 20 sites (Table 2) is

given in Fig. 2. Samples (sites) were grouped using a Bray-Curtis similarity matrix and hierarchical agglomerative clustering. The sites regarded as relict streams formed the first major group comprising Upper Serpentine Gorge, Giles Yard Spring and Talipata Springs. Serpentine Gorge also grouped within this cluster, which is possibly not surprising as it was separated by only 400 m (approximately) and a small waterfall from the Upper Serpentine site. Upper Redbank Gorge, Spencers Gorge and Berry Pass Springs formed a second cluster on the basis of the similarity of their macroinvertebrate fauna. None of the sites which clustered first contained fish, with the exception of Serpentine Gorge. Spencers Waterhole, the pool above Glen Helen, Trephina Gorge and Pioneer Creek formed a discrete group. These appeared to be the poorest sites with respect to water quality. The largest grouping comprised all the Ormiston sites, Redbank and Glen Helen gorges, Ellery Creek Big Hole, Redcliff Waterhole and Boggy Hole.

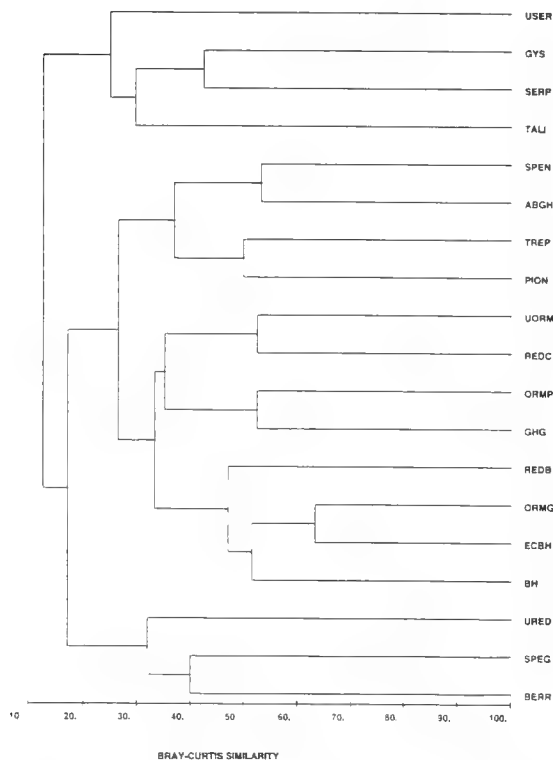


Figure 2. Dendrogram produced by hierarchical clustering of macroinvertebrate communities at waterbodies in the West MacDonnell Ranges and other Central Ranges localities, using group average linking of Bray-Curtis similarities. Site codes are defined in Table 1.

A slightly different clustering pattern was evident when all sites, from both the West MacDonnell Ranges 1993/94 study and the George Gill Range 1986/87 study were included in a single analysis (Fig. 3). Upper Serpentine separated first, however, it must be noted that only a small number of species were recorded from this site due to the difficulties with sampling (this site could only be reached by swimming through the gorge). All George Gill Range sites were within the same group at the second division, indicating that the fauna of these sites were more similar to each other than to the majority of the West MacDonnell Range sites, with the exception of the relict stream sites. Talipata Springs, Giles Yard Spring, Giles Spring and Serpentine Gorge also grouped with the George Gill Range sites. The remaining sites formed groups which were essentially identical to those of the previous dendrogram (Fig. 2).

Ordination of the West MacDonnell Ranges sites (Fig. 4) on the basis of their macro-

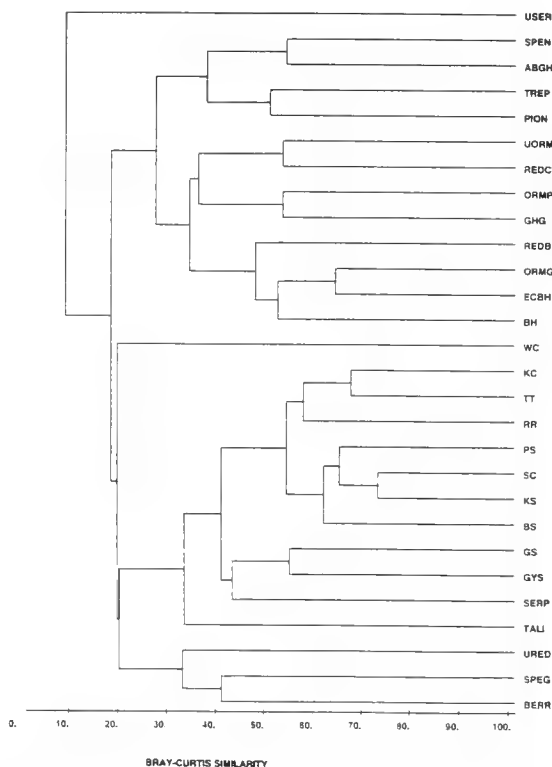


Figure 3. Dendrogram produced by hierarchical clustering of macroinvertebrate communities at waterbodies in the West MacDonnell Ranges, George Gill Range and other Central Ranges localities using group average linking of Bray-Curtis similarities. Site codes are defined in Table 1.

invertebrate fauna using non-metric multi-dimensional scaling, from the PRIMER package MDS, revealed the interrelationships between sites. Three relict stream sites, Giles Yard Spring, Upper Serpentine Gorge and Talipata Springs, plus Upper Redbank Gorge were located some distance from the main group which comprised all other sites.

Ordination of the same sites, by MDS, on the basis of environmental variables (Fig. 5), revealed a similar but more discrete separation into two groups. Giles Yard Spring, Upper Serpentine Gorge, Talipata Springs and Upper Redbank Gorge were all located towards the righthand side of the plot. Fish were absent at these sites and conductivities were low. The remaining sites, which were all located towards the left side of the plot contained fish. A gradation in conductivity was also evident within these groups with the freshest sites at the top of the plot and the saltiest at the base.

An ordination of all sites from both the West MacDonnell Ranges 1993/94 study and the George Gill Range 1986/87 study is given in Fig. 6. Some sites, in particular Wanga Creek (in the GGR), Trephina Gorge, Pioneer Creek, the pool below Ormiston Gorge, Upper Redbank Gorge and Spencers Gorge are clearly outliers. Relict stream sites from both regions were located together on the left side of the plot.

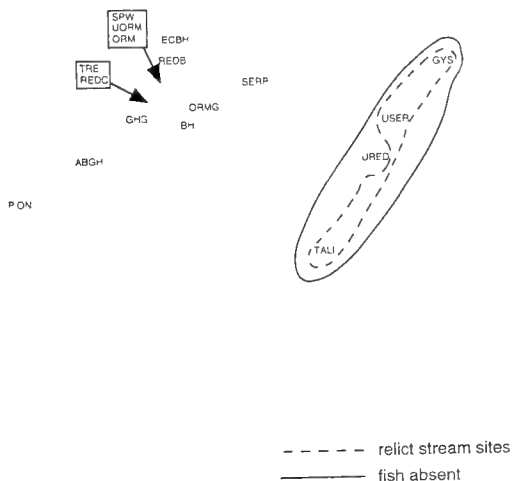


Figure 5. Ordination of waterbodies in the West MacDonnell Ranges, on the basis of environmental variables (conductivity, pH, presence/absence of fish, substratum and exposure) using non-metric multi-dimensional scaling (MDS). Site codes are defined in Table 1.

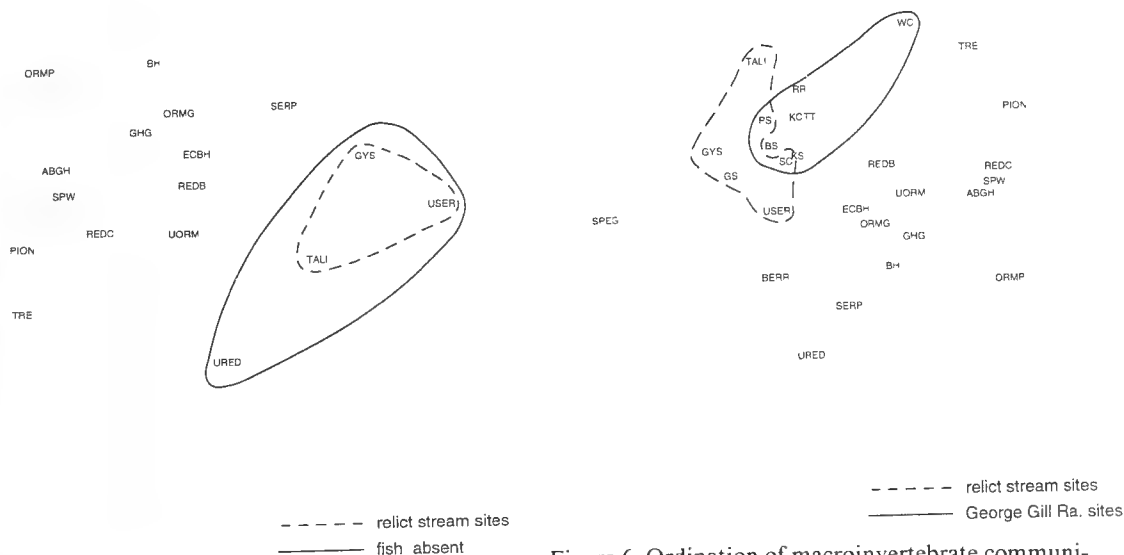


Figure 4. Ordination of macroinvertebrate communities at waterbodies in the West MacDonnell Ranges, using non-metric multi-dimensional scaling (MDS). Site codes are defined in Table 1.

Figure 6. Ordination of macroinvertebrate communities at waterbodies in the West MacDonnell Ranges and George Gill Range, using non-metric multi-dimensional scaling (MDS). Site codes are defined in Table 1.

Discussion

As noted by Williams and Siebert (1963), the waterbodies of the West MacDonnell Ranges are probably the most isolated freshwater habitats in Australia, being separated by arid or semi-arid lands from the high rainfall regions of the north by approximately 1000 km and from the southeast and southwest by approximately 1600 km. Despite the isolation, and the aridity, the waterbodies support a rich and abundant invertebrate fauna, although species richness appears to be slightly lower than that of the waterbodies of the George Gill Range, to the southwest, where 109 taxa were recorded by Davis et al. (1993). The fauna of the West MacDonnell Ranges is markedly different to that of the mound springs of South Australia. The mound springs to the south and west of Lake Eyre are moderately saline environments with conductivities ranging from 5,600 to 14,700 uS/cm (Mitchell 1985). Important elements of the fauna of these springs, such as the phreatoid isopod, *Phreatomerus latipes*, hydrobiid gastropods and an unidentified amphipod (Mitchell 1985) were not present in the West MacDonnell Ranges.

Previously, Davis et al. (1993) had suggested that a small proportion of the fauna present at the George Gill Range appeared to be a relictual stream fauna. This supported Chippendale (1963) who regarded some of the ranges of central Australia, including the MacDonnell, James, Krichauff and George Gill Ranges as relict areas 'where plants of a higher rainfall period have survived'. These results also supported the work of Latz et al. (1981) who found the George Gill Range to be very floristically rich with a small but significant percentage of the flora being rare or of relict distribution.

The present study of the West MacDonnell Ranges, together with that of Davis et al. (1993) indicates that a total of nine relict stream sites, Giles Yard Spring, Giles Spring, Upper Serpentine Gorge, Bowmans Gap, Upper Hugh Gorge, Talipata Springs, Talipata Gorge, Stokes Creek and Penny Springs, are now known within the Central Ranges based on the occurrence of the waterpenny, *Sclerocyphon fuscus* (Coleoptera: Psephenidae) an obligate, rocky stream invertebrate. Waterpennies graze the biofilm associated with rocky substrates and so are restricted to cobble and pebble, rather than sand or mud, substrates. Davis et al. (1993) suggested that *S. fuscus*, which also occurs in South Australia and Victoria, would not be capable of dispersal

across the large tracts of arid land that now separate the Central Ranges from the other localities where it occurs in southern Australia. This species, and several others, appear to be members of a relictual stream fauna that have persisted since the interior of the continent was much wetter than it is today.

The occurrence of the waterpenny in central Australia is not a recent discovery, however the occurrence of a number of populations spanning a region of several 100 km in area was not previously known. Spencer (1896: 77–78) noted the presence of 'a curious Orthopteran insect resembling a small flattened-out cockroach which adheres almost as closely to the surface of submerged leaves as a limpet to a rock' at Penny Springs in the George Gill Range. This description more closely describes a waterpenny, than any other aquatic invertebrate.

The restriction of the distribution of the genus *Sclerocyphon* to primarily southern and coastal regions of Australia (Fig. 7) indicates a Gondwanan origin. Reconstruction of the phylogenetic history of the waterpenny genus *Sclerocyphon* places *S. fuscus* in one of the most recently derived species groups (Davis, 1986), suggesting that dispersal of this species may have occurred during a pluvial phase of the Quaternary, rather than earlier in the Tertiary. Dispersal of this species from localities in coastal South Australia and western Victoria is most likely to have

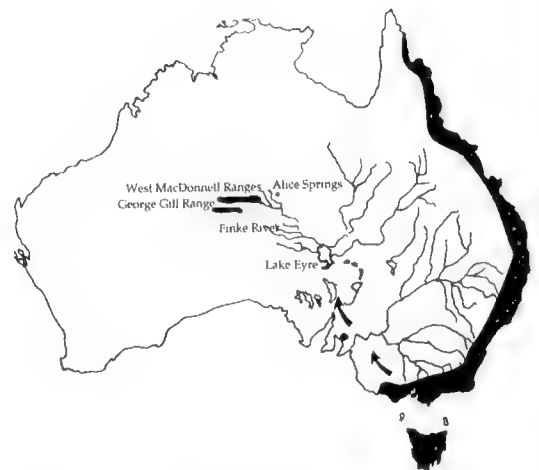


Figure 7. Currently known distribution of waterpennies (genus *Sclerocyphon*) and possible route of dispersal of *Sclerocyphon fuscus* from southeastern Australia to the headwaters of the Finke River, prior to the onset of aridity in central Australia.

occurred through the Finke River system (Fig. 7) when it existed as a major flowing water system in central and southern Australia, possibly as recently as 18 000 years ago.

Species such as the case dwelling chironomid, *Dicortendipes*, the larval dipteran, Stratiomyidae, which clings to wet rock walls, the large golden-spotted beetle, *Sandracottus bakewelli* and the large backswimmer, *Enithares*, and the dragonflies, *Hemicordulia flava*, *Orthetrum migratum* and *Notolibullela bicolor*, all appear to be predominantly associated with relict stream sites. The low conductivities recorded at the relict stream sites suggest that the presence of permanently discharging groundwater is vital to the maintenance of these habitats. The groundwater that supports the relict stream communities also supports mosses and ferns and further work is needed to fully document the plant communities associated with relict stream habitats. The presence of damp terrestrial microhabitats at these relict sites may be an important environmental requirement for *S. fuscus*, as both the pupa and adults of species recorded elsewhere in Australia are often associated with damp moss and leaf litter.

The presence, or absence, of fish appears to be important in determining invertebrate community structure in the waterbodies of the West MacDonnell Ranges. Different invertebrates were present at sites where fish were present compared to those where fish were absent. The lack of large numbers of introduced species of fish in central Australian waterbodies suggests that the composition of fish communities in this region may be largely unchanged since European settlement. The lack of exotic species, in comparison to those of waterbodies in more populous regions of Australia, may be explained by low human population densities within the region, reduced dispersal opportunities and the highly variable hydrological regimes and physico-chemical attributes of many arid zone waterbodies. It is extremely important, for the conservation and preservation of the aquatic ecosystems, that exotic fish are not introduced into central Australia at any time in the future.

Spencer and Hall (1896) recorded the yabby, *Astacopsis bicarinatus*, now recognised as *Cherax destructor*, from Running Waters and Hermannsburg and noted that it occurred frequently in waterholes along the Finke River. Anecdotal information suggests that the distribution of the yabby in central Australia has increased since the time of the Horn Expedition

as a result of active translocations. No record of the yabby in the George Gill Range was given by Spencer and Hall (1896) but it appears to have been introduced to Bagot Creek in the 1930s and Stokes Creek in the 1960s to provide a food source and for recreational fishing (Davis et al., 1993). The translocation of yabbies in central Australia mirrors widespread translocations elsewhere in Australia (Horwitz and Knott, 1995) but the introduction of yabbies to waterbodies where they did not previously occur must be regarded as a serious threat to the conservation of the original aquatic communities through both habitat alteration and potential competition.

European settlement, and the advent of the pastoral industry, have had a major and continuing effect within the region. The use of waterholes as drinking points by introduced vertebrates associated with the pastoral industry, including cattle, horses, camels and donkeys has severely degraded many waterbodies, particularly within the lower regions of the Central Ranges. Trampling of banks and excess algal growth as a result of nutrient enrichment are evident at many waterbodies, particularly those that lie outside the West MacDonnell National Park. Nutrient enrichment may also have promoted the growth of submerged aquatics such as *Myriophyllum* at the expense of other species such as *Potamogeton* and *Vallisneria*. Similarly, the spread of the bulrush, *Typha*, is promoted by disturbed and nutrient-rich conditions.

As more people visit central Australia the demand for water for consumption, sanitation and other associated support activities (swimming pools, gardens, aquaculture ventures, etc) increases. As noted by Shepard (1993), water to support these activities has to come from nearby sources or associated aquifers to be economically feasible. There is a very real risk that human uses will compete with aquatic ecosystems for the limited supplies of water present in arid Australia. This risk must be acknowledged and addressed to ensure that overpumping of groundwater aquifers does not occur.

Shepard (1993) noted, with regard to North American desert springs, that 'with few exceptions, aquatic biologists have avoided work in deserts. The result is that a high diversity fauna full of vicariant strandings and speciations, unusual adaptations and varying responses to a harsh environment, remains unstudied.' Replace the word 'desert' with 'arid zone' and the same statement can be applied to the waterbodies of central Australia. Comparison of the

records of the Horn Expedition with the results of this study and other recent research (Davis, in press) suggests that the aquatic fauna of central Australia has essentially survived the impacts of European settlement, despite problems such as nutrient enrichment and bank erosion. The challenge is to ensure that these communities, particularly the relictual stream communities, continue to survive undiminished by human activities.

Acknowledgements

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References

- Blackburn, T., 1896. Coleoptera. Pp. 254–261 in Spencer, W.B. (ed.), *Report on the work of the Horn Scientific Expedition to central Australia*, Part 2. Melville, Mullen and Slade: Melbourne.
- Clarke, K.R. and Warwick, R.M., 1994 Change in marine communities — an approach to statistical analysis and interpretation. Plymouth Marine Laboratory: Plymouth.
- Chippendale, G.M., 1963 The relic nature of some central Australian plants. *Transactions of the Royal Society of South Australia* 86: 31–34.
- Crowley, L.E.M. and Ivantsoff, W., 1990 A review of species previously identified as *Craterocephalus cyrestii* (Pisces: Atherinidae). *Proceedings of the Linnean Society of NSW* 112: 87–103.
- Davis, J.A., 1986. Revision of the Australian Psephenidae (Coleoptera): systematics, phylogeny and historical biogeography. *Australian Journal of Zoology, Supplementary Series* 119: 1–97.
- Davis, J.A., in press. Aquatic ecosystems in central Australia: comparison of recent records of fishes and invertebrates with those of the Horn Expedition. In: Morton, S.R. and Mulvaney, D.J. (eds), *Exploring central Australia: society, the environment and the 1894 Horn Expedition*. Surrey Beatty and Sons: Chipping Norton.
- Davis, J.A., Harrington, S.A. and Friend, J.A., 1993. Invertebrate communities of relict streams in the arid zone: the George Gill Range, central Australia. *Australian Journal of Marine and Freshwater Research* 44: 483–505.
- Gibson, D.F. and Cole, J.R., 1993. Vertebrate fauna of the West MacDonnell Ranges, Northern Territory. *Conservation Commission of the Northern Territory Report*. Alice Springs.
- Glover, C.J.M., 1982. Adaptations of fishes in arid Australia. Pp. 241–246 in: Barker, W.R. and Greenslade, P.J.M. (eds), *Evolution of the flora and fauna of arid Australia*. Peacock Publications: South Australia.
- Glover, C.J.M. and Sim, T.C., 1978. A survey of Australian ichthyology. *The Australian Zoologist* 19: 245–256.
- Horwitz, P. and Knott, B., 1995. The distribution and spread of the yabby *Cherax destructor* complex in Australia: speculations, hypotheses and the need for research. *Freshwater Crayfish* 10: 81–91.
- Keast, A., 1959. Relict animals and plants of the MacDonnell Ranges. *Australian Museum Magazine* 13: 81–86.
- Kodric-Brown, A. and Brown, J.H., 1993. Highly structured fish communities in Australian desert springs. *Ecology* 74: 1847–855.
- Larson, H.K. and Martin, K.C., 1989. *Freshwater fishes of the Northern Territory*. Northern Territory Museum of Arts and Sciences: Darwin.
- Latz, P.K., Johnson, K.A. and Gillam, M.W., 1981. *A biological survey of the Kings Canyon area of the George Gill Range*. Internal report. CCNT, Alice Springs.
- Mitchell, B.D., 1985. Limnology of mound springs and temporary pools, south and west of Lake Eyre. Pp. 51–63 in: Greenslade, J., Joseph, L. and Reeves, A. (eds), *South Australia's Mound Springs*. Nature Conservation Society of South Australia: Adelaide.
- Shepard, W.D., 1993. Desert springs — both rare and endangered. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3: 351–359.
- Spencer, W.B. (ed.), 1896. *Report on the work of the Horn Scientific Expedition to central Australia*, Part 2. Melville, Mullen and Slade: Melbourne.
- Spencer, W.B. and Hall, M.A., 1896. Crustacea. Pp. 227–248 in: Spencer, W.B. (ed.), *Report on the work of the Horn Scientific Expedition to central Australia*, Part 2. Melville, Mullen and Slade: Melbourne.
- Tate, R., 1896. Mollusca. Pp. 181–226 in: Spencer, W.B. (ed.), *Report on the work of the Horn Scientific Expedition to central Australia*, Part 2. Melville, Mullen and Slade: Melbourne.
- Thompson, R.B., 1991. *A guide to the geology and landforms of central Australia*. Northern Territory Geological Survey: Darwin.

- Watson, J.A.L., 1974. The distributions of Australian dragonflies (Odonata). *Journal of the Australian Entomological Society* 13: 137-49.
- Watson, J.A.L., Theischinger, G. and Abbey, H.M., 1991. *The Australian dragonflies*. CSIRO: Canberra and Melbourne.
- Williams, W.D. and Siebert, B.D., 1963. The chemical composition of some surface waters in central Australia. *Australian Journal of Marine and Freshwater Research* 14: 166-175.
- Van Oosterzee, P., 1991. *The Centre — the natural history of Australia's desert regions*. Reed Books: Sydney.
- Zietz, A., 1896 Pisces. Pp. 176-180 in: Spencer, W.B. (ed.), *Report on the work of the Horn Scientific Expedition to central Australia, Part 2*. Melville, Mullen and Slade: Melbourne.

THE EFFECTS OF EUROPEAN SETTLEMENT ON THE BIODIVERSITY OF CHYDORID CLADOCERA IN BILLABONGS OF THE SOUTH-EAST MURRAY BASIN

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Abstract

Ogden, R.W., 1997. The effects of European settlement on the biodiversity of chydorid Cladocera in billabongs of the south-east Murray basin. *Memoirs of the Museum of Victoria* 56(2): 505-511

Assemblages of chydorid cladoceran headshields preserved in billabong sediments are analysed for changes in species abundance, richness and diversity from pre-European settlement to the present day. The fauna consists of at least 36 species. Species richness and diversity are lower in present day assemblages than before settlement, but this may be an artefact of increasing sedimentation rates. Although some species have declined markedly since European settlement, no definite extinctions have occurred. Chydorid Cladocera in billabongs may be pre-adapted to anthropogenic disturbance. Trends of decreasing abundance found in some species will need to be reversed if regional extinctions are to be avoided in the future.

Introduction

One of the aims of conservation is to preserve the biodiversity found in natural ecosystems. Normally, relatively undisturbed areas of an ecosystem serve as a benchmark for the natural biodiversity of the ecosystem. Knowledge of natural biodiversity is useful for a variety of purposes, including evaluating changes in biodiversity since European settlement, assessing how susceptible biota are to impacts from particular land use activities, identifying exotic species, and setting targets for ecosystem restoration.

Billabongs in the south-east Murray Basin contain diverse assemblages of invertebrates (Shiel, 1976; Shiel and Koste, 1983; Hillman and Shiel, 1991). However, farming and river regulation are so widespread in the Murray-Darling Basin that it is conceivable that there are no longer any billabongs in a pre European settlement condition to provide benchmarks for assessing the impacts of land use activities on biodiversity (cf. Walker and Hillman, 1977). Furthermore, the initiation of farming and other activities with the potential to affect biodiversity (e.g., fish introductions) preceded wide scale sampling of the region's invertebrate aquatic fauna (Ogden, 1996a).

In ecosystems such as billabongs that have been substantially altered by land use, fossil records provide an avenue for determining natural invertebrate biodiversity. Sediments deposited in slackwater areas preserve a record of resilient aquatic biota. The most common fos-

sils are from species with calcium carbonate tests (e.g., ostracods, molluscs) or decay-resistant chitinous body parts (e.g., cladocerans, chironomids, trichopterans).

The billabongs in this study are found in the valleys of the eastern Murray River and the lower Ovens and Kiewa Rivers (figure 1). This region includes stretches of unregulated river (Murray River Lake Hume, Ovens and Kiewa Rivers) and regulated river (Murray below Lake Hume). Present day farming intensity on the floodplain is variable but generally decreases downstream for both rivers. Farming activity was probably more intense on the floodplain in the middle 1800's than it is today (Ogden, 1996a). In addition to farming and river regulation, billabongs and the surrounding landscape have been affected by the spread of rabbits (Murray-Darling Basin Commission, 1990) and four exotic fish species (Cadwallader, 1986), fertiliser use (Ogden, 1996a), logging and ringbarking of trees, and possible changes in the fire regime (Murray-Darling Basin Commission, 1990).

Changes since European settlement environmental have lead to a widespread decline in submersed aquatic macrophytes in large, deep (2-5 m) billabongs of the region (Ogden, 1996a, b). Macrophytes are still common in shallow billabongs and in smaller billabongs nearer the headwaters of rivers, but the ecotype of a large, deep billabong with a fringe of submersed macrophytes has been replaced by a phytoplankton dominated billabong (Ogden, 1996a, b).

Billabongs are small, shallow lakes occurring on floodplains, and are characterised by large fluctuations in physicochemistry associated with natural changes in depth and flooding (Briggs et al., 1985; Tan and Shiel, 1993; Ogden, 1996a). High levels of disturbance due to natural factors in billabongs may confer a degree of resistance or resilience of billabong invertebrates to anthropogenic disturbance (cf. Yount and Niemi, 1990). The aim of this paper is to investigate the effects of the loss of the deep-water, vegetated billabong ecotype, or other changes in billabongs in the post European settlement period, on the biodiversity of, both within billabongs and regionally. Fossils of the families Chydoridae, Macrothricidae, Bosminiidae and Daphnidae are preserved in the sediments (Ogden, 1996a) but this paper is restricted to an analysis of the first two families only.

Methods

Sediment sampling and extraction of fossils

Sediment samples containing preserved Cladocera are from two sources. First, a single core was recovered from the deepest point in each of 7 billabongs (figure 1), and each core was subsampled for 1 cm sediment slices at various depths. Second, surface sediment samples (top 1 cm) from the profundal zone of 41 billabongs were obtained. Each surface sample consists of 3 subsamples that have been pooled. Ten of the billabongs are from the Murray River between Corryong, Victoria and Lake Hume, one from the Kiewa River, 22 from the Murray River between Lake Hume and Barmah Forest, and 8 from the Ovens River below Wangaratta. The locations of these billabongs are found in Ogden

(1996a). The cores were collected in 1992 and the surface sediment samples in 1993. The numbering of billabongs (figure 1) is based on a regional ecological survey (Ogden, 1996a). This system is retained for cross-referencing. The surface sediment samples come from a wider range of billabong types than the core-samples, which are from relatively deep (1.5–3.5 m), permanent-water billabongs only.

Cladocera were extracted from a 1–2 ml subsample of sediment. Details of the methods can be found in Ogden (1996a) or Frey (1986). Basically, the sediments were dispersed in hot KOH and the remains isolated by sieving and density separation. Slides were then prepared and the fossils are counted at 100x magnification.

Taxonomy

Headshields were used to differentiate chydorid species and identifications made by comparisons with published headshield illustrations or dissections of species collected from the study area. Many species have unique headshield morphometrics and pore arrangements (Frey, 1986), but some species, notably certain members of the genera *Chydorus*, *Biapertura*, *Alona* and *Ephemeroporus*, cannot be differentiated on the basis of their headshields (Ogden, 1996a). Headshields from such species are listed as undifferentiated or, if they appear to be closely related, assigned to species complexes.

Chronology

Billabong sediments deposited after c. 1870 are differentiated on the basis of the presence of pollen from the introduced tree genus *Pinus*. Settlement of the region by Europeans occurred in the middle 1800's, and trees of the genus *Pinus* were widespread and pollinating by 1870. Sediments lacking *Pinus* pollen are therefore considered to have been deposited before European settlement. ^{210}Pb dating in two cores has supported the use of *Pinus* as a postsettlement marker (Ogden, 1996a).

Counting, analysis and statistics

A minimum of 50 chydorid headshields per sample were counted. Species richness and Shannon diversity (using natural logs; Begon et al., 1986) of chydorid assemblages were calculated.

The chydorid species assemblages were pooled into 3 periods for comparison: recent (1993), postsettlement (1870–1990) and presettlement (pre-1870). The recent period is made up of headshields from surface sediment samples of 41 billabongs. Five sediment samples

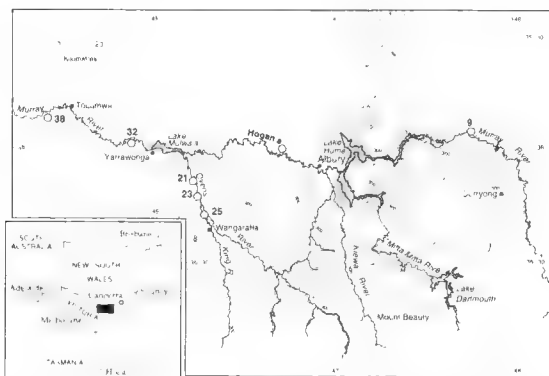


Figure 1. The study region. The locations of billabongs from which sediment cores were recovered are shown.

from three billabongs (numbers 23, 25 and 32) make up the postsettlement (1870–1990) period. Presettlement headshields are from 20 sediment samples deposited in 7 billabongs. For some analyses, presettlement assemblages were subdivided into upper presettlement (c. 1850) and lower presettlement samples (pre-1850). Presettlement samples are nearest, and pre-1850 samples furthest, in time-depth to the settlement boundary in cores. The pre-1850 samples are from six rather than seven billabongs due to preservation problems in the pre-1850 sample from billabong 21.

Differences in species richness and Shannon diversity of chydorid assemblages from recent, c. 1850 and pre-1850 time periods were investigated using linear mixed models. The random model was billabongs and observations within billabongs. The dependent variable in the fixed model was the assemblage measure (richness, diversity), and the independent variable the time period. An ANOVA was performed and the significance of the difference between means tested by calculating the F-probability of the variance ratio. For this analysis, the chydorid assemblages were restricted to the first 50 chydorid headshields encountered. Postsettlement (1870–1990) assemblages were excluded from modelling due to limited data.

Results

In all, 36 chydorid and one macrothricid species of are differentiated in the assemblages of headshields. The term ‘species’ here refers to both individual species and species complexes. Species richness is therefore probably underestimated. No attempt is made to identify the macrothricids to species since they do not appear to persist as fossils.

Increased decomposition is apparent in all cores following the onset of settlement, based on a loss of lustre and partial breakdown of some of

the remains. The macrothricid remains appear to be quite susceptible to organic decomposition; they are quite commonly represented by the outer rim of the headshield only. However, none of the chydorid species that increase in abundance towards the surface appear to be exceptionally susceptible to organic breakdown or fragmentation. Furthermore, decomposition and other taphonomic factors have not significantly altered the overall proportion of body parts, or the degree of fragmentation, between recent, post and presettlement chydorid assemblages, based on ANOVA modelling ($p=0.050$; Ogden, 1996a).

Considering only chydorids, up to seven species are present in recent assemblages that are not found in the presettlement assemblages (table 1). However, four of these are doubtful due to taxonomic uncertainties. The two uncertain *Alona* species are more distinctive end members of species complexes. The *Rak/Chydorus* species is only represented by one headshield, and a 4-porate species by two headshields. These may simply be mutants of *Rak/Chydorus* and *Alona*, respectively. The 4-porate species does not resemble *Oxyurella*. In contrast, only one doubtful species is found in the presettlement assemblages that is not found in the recent assemblages (table 1).

Large shifts in the abundance of common species in the region are apparent with European settlement (table 2). Undifferentiated species of *Chydorus*, *Biapertura*, and *Alona* are relatively more abundant following settlement, at the expense of *Rak/Ephemeroporus* cx. 1 (hereafter called *Ephemeroporus* cx. 1), *Ephemeroporus* cx. 2, and *Alonella excisa*. The decline of *Ephemeroporus* cx. 1 is noteworthy. Only one *Ephemeroporus* cx. 1 specimen was found in 2889 headshields from postsettlement and recent assemblages, compared to 8% relative abundance before settlement.

Table 1. Chydorid species found exclusively in either recent or presettlement assemblages.

In recent assemblages, not in presettlement assemblages:	
taxonomy certain	taxonomy uncertain
<i>Alona</i> sp. 1	<i>Alona pulchella</i> sp.1
<i>Alonella</i> sp.1	<i>Alona diaphana</i> sp.1
<i>Leydigia acanthocercoides</i>	<i>Rak</i> or <i>Chydorus</i> species
	Unknown genus or 4-porate mutants of <i>Alona</i>
In presettlement assemblages, not in recent assemblages:	
taxonomy certain	taxonomy uncertain
none	unknown genus related to <i>Alona</i>

Table 2. Abundance of common chydorid species in each time period.

time period	1993		1993		1870–1990		pre 1870	
no. billabongs	41		7		3		7	
total count	2635		408		254		1169	
species	no.	%	no.	%	no.	%	no.	%
<i>Chydorus undiff.</i>	920	35	88	22	83	33	77	7
<i>Biapertura undiff.</i>	490	19	149	36	48	19	242	21
<i>Alona undiff.</i>	605	23	89	22	23	9	88	8
<i>Rak/Ephemeroporous</i> cx. 1	1	~0	0	0	0	0	95	8
<i>Ephemeroporous</i> cx. 2	72	3	4	1	28	11	236	20
<i>Alonella excisa</i>	49	2	7	2	20	8	136	12

Table 3. Abundance of macrothric and minor chydorid species occurring in each time period. Common species are excluded from calculations of the percentage of minor species.

time period	1993		1993		1870–1990		pre 1870	
no. billabongs	41		7		3		7	
total count	498		71		52		295	
CHYDORIDAE	no.	% of minor species	no.	% of minor species	no.	% of minor species	no.	% of minor species
Little change in relative abundance:								
<i>Graptoleberis testudinaria</i>	70	15.4	13	18.3	7	13.5	30	10.2
<i>Biapertura setigera</i>	22	4.8	2	2.8	1	1.9	13	4.4
<i>Biapertura affinis</i>	38	8.4	4	5.6	5	9.6	17	5.8
<i>Biapertura</i> sp. 7	10	2.2	2	2.8	2	3.9	9	3.1
<i>Alona quadrangularis</i>	47	10.3	13	18.3	10	19.2	28	9.5
<i>Monope or Ephemeroporus</i>	10	2.2	1	1.4	0	0	3	1.0
<i>Pseudochydorus globosus</i>	6	1.3	0	0	0	0	2	0.7
<i>Daydaya macrops</i>	8	1.8	2	2.8	1	1.9	2	0.7
<i>Oxyurella</i> sp.	4	0.9	1	1.4	0	0	5	1.7
Decreasing relative abundance:								
<i>Biapertura</i> sp. 1	20	4.4	2	2.8	6	11.5	38	12.9
<i>Biapertura</i> sp. 2	7	1.5	1	1.4	5	9.6	46	15.6
<i>Biapertura</i> sp. 3	1	0.2	0	0	0	0	10	3.4
<i>Camptocercus australis</i>	18	4.0	4	5.6	4	7.7	48	16.3
<i>Biapertura karua</i>	9	2.0	0	0	2	3.5	32	10.8
Increasing relative abundance:								
<i>Alona</i> cf. <i>diaphana</i>	16	3.5	1	1.4	2	3.9	0	0
<i>Biapertura</i> sp. 5	10	2.2	3	4.2	1	1.9	1	0.3
<i>Leydigia leydigi</i>	28	6.2	10	14.1	1	1.9	2	0.7
<i>Dunhevedia crassa</i>	14	3.1	3	4.2	1	1.9	2	0.7
<i>Leydigia acanthocercoides</i>	14	3.1	7	9.9	1	1.9	0	0
<i>Pleuroxis inermis</i>	54	11.9	2	2.8	0	0	1	0.3
<i>Kurzia</i> cf. <i>latissima</i>	7	1.5	0	0	0	0	1	0.3
<i>Alona</i> cf. <i>puchella</i>	6	1.3	0	0	0	0	0	0
<i>Alona</i> sp. 1	8	1.8	0	0	0	0	0	0
MACROTHRICIDAE								
All spp.	40	—	10	—	1	—	0	—

Of the 30 less common chydorid species, seven are too rare to detect trends with European settlement, and nine species change little in their relative abundance (table 3). Five species decrease in relative abundance following settlement, and nine species increase in relative abundance (table 3), although three of these are only found in recent sediments from billabongs that were not cored. Species with an increasing or decreasing trend in relative abundance usually have intermediate levels in 1870–1990 assemblages. Macrothricid fossils are found in 19 of the 41 recent assemblages, and are absent from presettlement assemblages (table 3).

Species richness of presettlement assemblages ranges from 10–16 species and diversity is 1.35 to 2.35 based on 50 to 101 headshields per sample. Recent (1993) assemblages have on average 1–4 less species than presettlement assemblages (table 4) and have lower diversity (table 5). Species diversity and richness do not vary significantly between c. 1850 and pre-1850 assemblages (tables 4 and 5).

Discussion

Shifts in the dominance of species in cladoceran assemblages from before European settlement to the present day (tables 1–3) are indicative of environmental change in billabongs. Either a change in the dominance of chydorid species in living communities has occurred, or increased decomposition of remains following settlement has altered the make-up of assemblages. However, greater decomposition of postsettlement assemblages has not increased fragmentation, or changes the proportion of body parts, or differentially affected the appearance of any one chydorid species, suggesting that the taphonomic effects are minor.

Historic increases in the dominance of *Chydorus sphaericus* have been considered as evidence for eutrophication in some northern hemisphere lakes (Frey, 1986). This may be the reason behind the increased dominance of undifferentiated *Chydorus* following European settlement (table 2). Indeed, several chydorid species have been found associated with floating material, including some indicators of eutrophication such as *Azolla* and floating algal mats (pers. obs. and Russ Shiel, pers. comm., 1996). However, chydorids were rare in the numerous plankton samples taken in the course of a limnological survey of billabongs (Ogden, 1996a), lending support to Shiel's (1976) opinion that they are littoral strays.

Species richness and diversity are lower in present day chydorid assemblages than in presettlement assemblages. Sedimentation rates appear to have increased postsettlement (Ogden, 1996a), so it is likely that the surface assemblages accumulated in a shorter time span than the presettlement assemblages. The presettlement samples may have more species because they represent longer time-slices than the surface assemblages, and compaction of deeper sediments accentuates this effect (Smol, 1981). Decreases in richness and diversity from presettlement to recent assemblages are not great enough to conclude they translate to differences in chydorid communities living at the time. At the least, though, it can be concluded that the richness and diversity of chydorid communities have not increased since settlement.

A number of species occur in present day billabongs that are not found before settlement (tables 4 and 5). There are three possible explanations: low preservation potential of these species, sampling of a broader range of billabong types for present day cladoceran assemblages compared to the 7 billabongs sampled for their presettlement assemblages, and the introduction of exotic species.

The macrothricid provide an example of taxa that do not preserve. Macrothricid headshields are reasonably common in surface sediments but are almost never found in deeper sediments (table 3), and where present, are usually decayed. As already noted, variation in the relative preservation potential of individual chydorid species is not readily apparent.

Pleuroxus cf. *inermis* is an example of a species that normally inhabits a billabong type different from those that were cored. The cored billabongs are all relatively deep, permanent water sites. *Pleuroxus* prefers shallow, ephemeral billabongs. Notable occurrences elsewhere are the Albury sewage treatment lagoon (Ogden, 1996a) and Pleistocene sediments from Cuddy Springs, NSW (pers. obs.). *Pleuroxus* cf. *inermis* therefore appears to thrive in highly disturbed billabongs, unlike the sites chosen for coring. *Kurzia* cf. *latissima*, *Alona* cf. *puchella* and *Alona* sp. 1 also seem to favour environments not found in the cored billabongs.

In contrast, *Alona* cf. *diaphana* and *Leydigia* sp. 2 (table 4) are fairly widespread, and occur in the cored billabongs and other deep or permanent-water billabongs. They are candidates for postsettlement introductions into the study region.

Table 4. Mean species richness of cladoceran assemblages.

number of billabongs	mean richness			difference in means \pm 2 s.e.	prob.
	1993	ca. 1850	pre 1850		
7	8.9	11.3		2.4 ± 1.4	0.015
6	8.3		12.7	4.3 ± 2.2	0.010
6		11.2	12.7	1.5 ± 1.8	0.165

Table 5. Mean species diversity of cladoceran assemblages.

number of billabongs	mean diversity			difference in means \pm 2 s.e.	prob.
	1993	ca. 1850	pre 1850		
7	1.55	2.08		$.53 \pm .23$	0.003
6	1.51		2.07	$.56 \pm .36$	0.028
6		2.05	2.07	$.02 \pm .28$	0.922

Regional biodiversity of the Chydoridae in billabongs has either increased or remained steady since European settlement. Species introductions may have been offset by regional extinctions in the *Ephemeroporus* complex 1. This complex is almost certainly composed of more than one species, based on major and minor pore arrangements (Ogden, 1996a), and yet only one headshield of this complex was found in over 2600 headshields identified from surface sediments. Some members of *Ephemeroporus* complex 1 have probably gone extinct in the region.

The relatively small changes in regional biodiversity since European settlement are noteworthy in light of the intense utilisation of the floodplain and the regional decline of macrophytes in deeper billabongs (Ogden, 1996a, b). Significantly, the single *Ephemeroporus* complex 1 headshield was found in one of the few remaining large, deepwater, vegetated billabongs left in the region. Overall, though, the regional diversity of chydorid does not appear to have suffered much from the loss of the 'large, deepwater, vegetated' billabong ecotype. It is possible that the chydorids were preadapted to the changes that occurred with settlement (Yount and Niemi, 1990) due to high levels of

natural disturbance in billabongs (cf. Brock, 1986; Ogden, 1996a).

In spite of presettlement regional chydorid biodiversity remaining intact, there is good reason to suspect that this situation will not persist. The reduction in abundance of some species and species complexes, such as *Ephemeroporus* complex 1, *Biapertura karua* and *Biapertura* sp. 3 appears to follow a declining trend through time. If this trend continues, some of the species will become regionally extinct.

Conclusions

Species richness and diversity of chydorid may have declined in billabongs after European settlement, but the possibility that this pattern is an artefact of increasing sedimentation rates cannot be eliminated. Overall, the biodiversity of chydorid has changed very little in billabongs of the south-east Murray Basin since European settlement, which is remarkable given the environmental impacts to billabongs in that time. This suggests a large degree of flexibility in the life strategy of chydorids in billabongs, possibly due to billabongs having a large amount of natural disturbance. However, some species are gradually declining in regional abundance, and if this trend continues, regional extinctions can be expected.

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References

- Begon, M., Harper, J.L. and Townsend, C.R., 1986. *Ecology: individuals, populations and communities*. Blackwell Scientific Publications: Oxford.
- Briggs, S.V., Maher, M.T., and Carpenter, S.M., 1985. Limnological studies of waterfowl habitat in south-western New South Wales. I. Water chemistry. *Australian Journal of Marine and Freshwater Research* 36: 59-67.
- Brock, M.A. 1986. Adaptations to fluctuations rather than to extremes of environmental parameters. Pp. 131-140 in: de Deckker, P. and Williams, W.D. (eds), *Limnology in Australia*. CSIRO, Dr. W. Junk: Melbourne.
- Cadwallader, P.L., 1986. Fish of the Murray-Darling system. Pp. 679-694 in: Davies, B.R. and Walker, K.F. (eds), *The ecology of river systems*. Dr. W. Junk: Dordrecht.
- Frey, D.G., 1986. Analysis. Pp. 667-692 in: Berglund, B.E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology*. John Wiley and Sons.
- Hillman, T.J. and Shiel, R.J., 1991. Macro- and micro-invertebrates in Australian billabongs. *Verhandlungen Internationale Vereinigung Limnologie* 24: 1581-1587.
- Murray-Darling Basin Commission, 1990. *River Murray riparian vegetation study*. Murray-Darling Basin Commission: Canberra.
- Ogden, R.W., 1996a. *The effects of farming and river regulation on billabongs of the eastern Murray River and lower Owens River*. Unpublished PhD thesis. ?University.
- Ogden, R.W., 1996b. Potential for the restoration of aquatic macrophytes in billabongs. Pp. 99-104 in: Rutherford, I. and Walker, M. (eds), *Proceedings of the First National Conference on Stream Management in Australia*. CRC for Catchment Hydrology.
- Shiel, R.J., 1976. Associations of entomostraca with weedbed habitats in a billabong of the Goulburn River, Victoria. *Australian Journal of Marine and Freshwater Research* 27: 533-49.
- Shiel, R.J. and Koste, W., 1983. Rotifer communities in northern and south-eastern Australia. *Hydrobiologia* 104: 41-47.
- Smol, J.P., 1981. Problems associated with the use of 'species diversity' in paleolimnological studies. *Quaternary Research* 15: 209-212.
- Tan, L.-W. and Shiel, R.J., 1993. Responses of rotifer communities to inundation. *Hydrobiologia* 255/256: 361-369.
- Yount, J.D. and Niemi, G.J. 1990. Recovery of lotic communities and ecosystems from disturbance: a narrative review of case studies. *Environmental Management* 14: 547-569.
- Walker, K.F. and Hillman, T.J., 1977. *Limnological survey of the River Murray in relation to Albury-Wodonga, 1973-1976*. Albury Wodonga Development Corporation: Wodonga.

AMPHIPOD (CRUSTACEA) DIVERSITY IN UNDERGROUND WATERS IN AUSTRALIA: AN ALADDIN'S CAVE

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Abstract

Bradbury, J.H. and Williams, W.D., 1997. Amphipod (Crustacea) diversity in underground waters in Australia: an Aladdin's cave. *Memoirs of the Museum of Victoria* 56(2): 513–519.

The presently known troglobitic and troglophilic (stygobiont) species of Australian aquatic amphipods are listed and discussed, and their geographical distributions are indicated. The 26 species known are predominantly in crangonyctoid and hadzioid families. Further undescribed species are referred to. The diversity is high and confirms Australia as a centre of stygobiont amphipod speciation. Explanations for the diversity include the considerable extent of karst, the frequent occurrence and extensive areas of former marine transgressions, and palaeoclimatic fluctuations. Attention is drawn to the usefulness of stygobiont amphipods as biogeographical tools, and to the need for their diversity in Australia to be noted in discussions, legislation and actions to conserve Australian biodiversity.

Introduction

Until relatively recently, our knowledge of the taxonomy of Australian freshwater amphipods (Crustacea: Amphipoda) was limited. Few species had been described, the extent of diversity was unrecognized, and most available species descriptions were in need of revision. Williams and Barnard (1988) began the initial revision needed with redescriptions of all known species and added descriptions of a few new species. Their efforts were continued in a second paper (Barnard and Williams, 1995). Both papers referred to subsurface as well as surface forms.

Taxonomic studies of the Australian freshwater amphipods are a long way from completion but the papers of Barnard and Williams and other recent studies have pointed to the existence of much greater diversity amongst surface forms than had been realised. They also point to the existence of greater biodiversity amongst subsurface forms than had been realised (Williams, 1986). The diversity of subsurface forms is confirmed by the studies of Knott (1983) and Bradbury and Williams (1995, 1996 a, b) and unpublished work on recent collections from caves and other underground waters in Western Australia, New South Wales and Tasmania. This diversity amongst subsurface forms is not surprising given both the paucity of previous studies and, more importantly, the fact that amphipods are known worldwide to be amongst the most widespread, abundant and diverse of subsurface aquatic invertebrates (Holsinger, 1991).

In this paper, our immediate intentions are to summarize the present status of our knowledge of the taxonomy of hypogean amphipods in Australia on the basis of described species, to provide some indication of the extent of diversity based on described species and undescribed material, and to offer some explanation for this diversity. Thus this paper provides a basis for discussion and should help achieve two, more general aims, namely:

1. to focus attention upon the usefulness of hypogean amphipods as biogeographical tools (given the nature of their ecology and environments) within an Australian context, and
2. to draw attention to the significant diversity of Australian hypogean amphipods at a time when considerable discussion is taking place at a variety of levels — State, Federal and international — on the conservation of biodiversity.

In these discussions, the diversity of hypogean amphipods should not be forgotten; whilst caves and other subsurface waters do not have the faunal diversity of surface waters, and of course lack plants, within the animal groups that do occur there (see, for example, Culver, 1982, and Barr and Holsinger, 1985), much speciation has taken place. Holsinger (1991, 1994a) has previously noted the global importance of hypogean amphipods for biogeographical studies, and Knott (1985) has noted their interest in Australia. Australian speleologists have long recognized the need for caves to be conserved and their fauna protected on the basis of both bio-

logical and geomorphological criteria. Governments have generally acted sympathetically to this need for cave protection and conservation.

In passing, we also mention the recent recognition of much higher diversity than expected in other bodies of inland water in Australia that — like underground waters — have generally received less attention from biologists than permanent fresh waters near major metropolises. These waters include salt lakes, temporary streams and freshwater lakes, and other bodies of surface water in arid and semi-arid regions. Recent work has indicated that considerable biodiversity occurs within such localities (e.g., see Frey, 1991; Timms, 1993; Comin and Williams, 1994). Their fauna, however, does not usually involve amphipods as these crustaceans are more or less confined to permanent, fresh waters. It does involve a comprehensive range of other invertebrate groups.

Present status of the hypogean (stygobiont) amphipod fauna

Table 1 lists all described species recorded thus far from either underground waters (caves, boreholes) or springs near their source. It lists two principal sorts of taxa: those which have been recorded from underground waters (including springs) and nowhere else (obligate stygobionts or troglobites *sensu* Barr and Holsinger, 1985); and those recorded from both underground and surface waters (facultative stygobionts or troglaphiles). In total, the table lists over 30 species of which half can be regarded as troglobites and half, troglaphiles. All are endemic. On the basis of described species, therefore, approximately 60 per cent of the total amphipod diversity of Australian inland waters can be found in subsurface waters. This figure is far higher than the global figure of 13 per cent given by Holsinger (1993) for the approximate fraction of all described amphipod species that are stygobionts. Our percentage is undoubtedly inflated by our concentration on stygobionts during recent studies. It seems likely that more balanced and comprehensive studies of both hypogean and epigean species will lead to some correction of this high figure towards a lower value.

With regard to the systematic positions of the species listed in the table, it is immediately obvious that most belong to the three groups identified by Holsinger (1993) as those of most importance so far as hypogean amphipod diver-

sity is concerned worldwide, namely, the crangonyctoids, the hadzioids *s. l.* and the bogidiellids.

The geographical distribution of the species listed in Table 1 is indicated in Fig. 1. An obvious point to emerge from this figure is the large number of stygobiont species recorded from Western Australia. Of particular note in this respect is the extraordinarily large number described from Barrow Island, a relatively small offshore island. Species recorded from this island comprise those collected from boreholes (species of *Nedsia* and *Bogadomma australis*), and two species from an anchialine cave — that is, a coastal cave under marine influence — (*Lia-goceradocus* spp.). None of the *Nedsia* species was found co-existing with another (but note paucity of specimens available), and all at present are known only from one locality each, the type locality. Apart from the facultatively subterranean *Austrochiltonia australis*, which is also a common and widespread surface form, other species listed in the table and figured in the map are likewise recorded from either a single locality or a restricted area. An absence of sympatry appears to be generally characteristic of stygobiont amphipods elsewhere too.

A less obvious point shown by Fig. 1 is that the distributions of hypogean amphipods extend more to the north in Australia than do those of



Figure 1. Geographical distribution of stygobiont amphipods in Australia. 1–12, hadzioids; 13, *Bogadomma*; 14–28, crangonyctoids. *Austrochiltonia australis*, *Phreatochiltonia anapthalma* and *Pseudomoera fontana* omitted.

Table 1. Systematic position and geographic distribution of Australian subterranean amphipods. The index numbers relate to Fig. 1.

Taxon	Distribution	Habit	Index no.
HADZIOIDS			
Melitidae			
<i>Nedsia straskraba</i> Bradbury & Williams	Barrow Island	troglobite	1
<i>N. fragilis</i> Bradbury & Williams	Barrow Island	troglobite	2
<i>N. humphreysi</i> Bradbury & Williams	Barrow Island	troglobite	3
<i>N. hurlberti</i> Bradbury & Williams	Barrow Island	troglobite	4
<i>N. urifimbriata</i> Bradbury & Williams	Barrow Island	troglobite	5
<i>N. macrosculptilis</i> Bradbury & Williams	Barrow Island	troglobite	6
<i>N. sculptilis</i> Bradbury & Williams	Barrow Island	troglobite	7
<i>Liagoceradocus subthalassicus</i> Bradbury & Williams	Barrow Island	anchialine troglobite	8
<i>Liagoceradocus branchialis</i> Bradbury & Williams	North West Cape	anchialine troglobite	9
<i>Nedsia douglasi</i> Barnard & Williams	North West Cape	troglobite	10
<i>Brachina invasa</i> Barnard & Williams	Flinders Ranges	hyporheic interstitial	11
<i>Nurinna Cave Melita</i> like	Nullabor Plain	troglobite	12
BOGIDIELLIDS			
Bogidiellidae			
<i>Bogadomma australis</i> Bradbury & Williams	Barrow Island	troglobite	13
CRANGONYCTOIDS			
Paramelitidae			
<i>Hurleya kalamundae</i> Straskraba	SW Australia	troglobite	14
<i>Protocrangonyx fontinalis</i> Nicholls	Darling Range, WA	troglophile	15
<i>Uroctena westralis</i> (Chilton)	nr Perth W A	troglophile	16
<i>Totgammarus eximius</i> Bradbury & Williams	SW Australia	troglophile	17
<i>Chillagoe thea</i> Barnard & Williams	N Queensland	troglobite	18
<i>Giniphargus pulchellus</i> Karaman & Barnard	Gippsland Vic	troglobite	19
<i>Austrogammarus species</i> Barnard & Karaman	Tasmania	troglophile	20
<i>Austrogammarus smithi</i> Williams & Barnard	Tasmania	troglophile	24
<i>Antipodeus antipodeus</i> (G.W.Smith)	Tasmania	troglophile	21
<i>Antipodeus wellingtoni</i> (G.W.Smith)	Tasmania	troglophile	22
<i>Antipodeus franklini</i> Williams & Barnard	Tasmania	troglophile	23
<i>Uronyctus longicaudus</i> Stock & Iliffe	SE South Australia	troglobite	25
Perthiidae			
<i>Perthia acutitelson</i> Straskraba	SW Australia	troglophile	26
Neoniphargidae			
<i>Neoniphargus obrieni</i> Nicholls	Mt Buffalo, Vic.	possible troglophile	27
<i>Neoniphargus</i> spp. Stebbing	Tasmania	troglophile	28
CEINIDS			
Ceinidae			
<i>Phreatochiltonia anapthalma</i> Zeidler	Mound spring, SA	poss troglobite	29
<i>Austrochiltonia australis</i> (Sayce)	cosmopolitan	troglophile	30
EUSIRIDS			
Eusiridae			
<i>Pseudomoera fontana</i> (Sayce)	SE Australia	troglophile	31

any surface aquatic amphipod. Thus, those from Barrow Island in Western Australia and *Chillogoe thea* in Queensland lie many hundreds of kilometres north of areas where surface amphipods occur. It is not difficult to provide an explanation of this; freshwater amphipods are not common in subtropical and tropical waters and only subterranean waters in these regions provide the lower temperatures and more stable environmental conditions required to support amphipod populations. It may be noted that not all northern and apparently suitable subtropical subsurface waters in Australia contain amphipods. The Cutta Cutta caves near Katherine, Northern Territory, for example, do not appear to be inhabited by amphipods; a recent and diligent search for them by one of us (WDW) failed to locate any specimens although considerable material of the atyid shrimp which do inhabit the caves was collected (*Parisia* spp.; see Williams, 1964). Perhaps the water in this cave system is too warm, the atyids too powerful a competitor, or there was no available ancestral surface form. No amphipods, likewise, have been collected from caves in the Kimberly region of Western Australia (Humphreys, 1995).

As for geographical patterns, three are obvious and accord with the broad biogeographical patterns postulated by Holsinger (1994a) for all subterranean amphipods and perhaps other malacostracans. These patterns are:

1. that shown by stygobionts derived from old freshwater ancestors (limnostygobionts);
2. that shown by stygobionts derived from marine ancestors, and
3. that shown by stygobionts inhabiting coastal waters with marine affinities and clearly derived from closely allied marine ancestors (thalassostygobionts or 'crawl-outs').

The process involved in pattern 3 is often referred to as 'stranding'. Crangonyctoid species clearly exhibit pattern 1, hadzioid species, pattern 2, and *Liagoceradocus* species, pattern 3. Other Australian stygobionts are less easily assigned to a particular pattern, but *Pseudomoera fontana* at least, given its marine taxonomic affinities and despite its entirely freshwater distribution, would appear to exhibit pattern 3. Fig. 2 indicates how close the correlation between distribution of stygobiont amphipods derived from hadziid ancestors is with areas of marine transgression and, conversely, of those with crangonyctoid ancestors and areas not inundated before or during the Cretaceous.



Figure 2. Marine transgressions in Australia during the Cretaceous (119–114 million years ago). Redrawn from Paine (1990). Areas free of inundation shaded.

The ecological nature of subsurface waters inhabited by species here considered as stygobionts covers a considerable range in type. Avoiding the plethora of technical terms that have been applied to subsurface waters, included are freshwater streams and lakes in inland caves in calcareous karst, coastal anchialine caves containing marine or brackish water, springs, mud or plant detritus on the bottom of surface waters which are in obvious continuity with the water table in unconsolidated substrata, and interstitial (hyporheic) water associated with streams. The collection of material from such a diversity of habitats itself demands diversity. For example, cave forms have been collected from open water by sweep nets or by baiting, forms in interstitial waters by pumping, and spring species by placing nets over surface outlets for extended periods (collections of *Brachina invasa* were made by placing a collecting net over the outlet of a spring for 12 hr).

The diversity of the hypogean amphipod fauna

On the basis of described species alone (Table 1), it is obvious that significant diversity exists amongst amphipods found in subsurface waters in Australia. How much more diverse will this fauna prove to be when further investigations have taken place? We have reason to believe that the answer is that it will prove to be substantially more diverse. This response is based in part on

our possession of further undescribed material from underground waters and including at least three new species from Western Australia, two from Queensland, and three from New South Wales (see also Eberhard et al., 1991). We believe it doubtful, however, that the number of species of hypogean amphipods in Australia will ever reach the numbers found in the two most diverse regions of the world in so far as this group is concerned, that is, the central-southern European — Mediterranean region and the eastern and southern North American — West Indian region. Even so, it is already clear that our increased knowledge of the diversity of hypogean amphipods in Australia confirms, as indicated, Holsinger's (1993) view that southern Australia is a region of significant diversity for this group. However, unlike the genera:species ratios found in the two regions of highest diversity mentioned, where the usual pattern is one of many species per crangonyctoid genus and few species per hadzioid genus, the pattern in Australia appears to be different, with many species per genus an obvious pattern for at least some hadzioid genera, and few species per genus for most crangonyctoid genera.

The causes of diversity

Two issues are involved in considering this matter. First, the factors that have led to the evolution of stygobiont amphipods in Australia, and second, those factors responsible for the high diversity.

The first set of factors are of relatively little interest in the present context; it may be presumed that the evolutionary routes followed by stygobiont amphipods in Australia are similar to those followed elsewhere by such organisms. Thus, all originated from surface forms by regressive evolution — irrespective of whether selection, the accumulation of neutral mutations, or genetic drift was the more important in this process (Culver, 1982) — after isolation from surface forms had occurred following sea-level change, the onset of climatic aridity, or a given geomorphological event. A number of evolutionary steps have been proposed through which populations pass as stygobiont species evolve. As a general rule, three broad ones can be recognized to accommodate the evolution of stygobionts from both inland and marine ancestors (Holsinger, 1994a). The first is inclusive of troglaphiles with few if any troglomorphic features. *Neoniphargus obrieni* provides an example. The second also include

troglaphiles but these do exhibit some troglomorphic features. Various species of *Antipodeus* provide examples. The third step includes troglaphites with clear troglomorphy. *Hurleya kalamundae*, *Nedsia* species, and *Protocrangonyx fontinalis* are some examples.

Of much greater interest are those factors responsible for the high diversity. In this connection it is instructive to determine those features held in common by the two regions of greatest stygobiont amphipod diversity, the central-southern European — circum Mediterranean region and the eastern and southern North American — West Indian region. In both regions, the following features are both held in common and regarded as significant in promoting the development of high diversity (Holsinger, 1994a): a former proximity to the Tethys Sea, the lack of extensive glaciation during the Pleistocene, large areas of karst, and widespread marine transgressions in the late Mesozoic and Cainozoic. To a not inconsiderable degree, *these features also characterise large parts of the Australian continent*. Over much of the Mesozoic, the Tethys Sea lay west of Australia; apart from the highlands of Tasmania and small areas of the highest mountains in the south-east of the mainland, the Australian continent was free of ice during the Pleistocene; and marine transgressions covered large areas of the Australian continent during the early Cretaceous (Fig. 2). The only difference, and one of degree not kind, is the extent of karst in Australia. Karst does occur widely in Australia (Jennings, 1985; Mathews, 1985), but continuously extensive areas are confined to the Nullabor Plain and the lower Murray Valley, with only relatively minor occurrences elsewhere (included here is the Fitzroy Basin of Western Australia, the Coolman Plain, Jenolan and Wee Jasper areas of New South Wales, the Buchan caves area of Victoria, the Mole Creek area of northern Tasmania, and the Barkly Basin of Queensland).

The evolution of stygobionts does not depend entirely upon the presence of karst, but there is little doubt that it does promote their evolution and the development of diversity. In any event, we believe that the features listed above, including the occurrence of karst — albeit it to an extent more limited than in the southern Europe — Mediterranean and North American — West Indian regions — have been important in producing the observed diversity of the Australian stygobiont amphipod fauna. Also important, we believe, has been both:

1. *continental drift* during which Australia first broke free from Gondwana and then passed through a series of quite distinct climatic zones during the Cainozoic, and
2. *palaeoclimatic fluctuations* including periods of aridity which, in conjunction with allied sea-level changes for coastal populations, would have served to isolate surface and sub-surface populations of a species and have led to the development of discrete drainage basins.

A succession of favourable (wetter and colder) and unfavourable (drier and warmer) climates could easily have provided mechanisms promoting stygobiont speciation as epigeal populations were driven to seek subterranean refugia. It may also be that some troglomorphic forms (lacking eyes) now found in surface waters actually represent the return to epigeal conditions of hypogean forms in the absence of surface competitors, the latter having become extinct during former unfavourable conditions. It is not possible, for eyes, once lost, to be regained.

Finally, some explanation should be offered for the extraordinary diversity of stygobionts on Barrow Island. The most likely one is that after stranding, ancestral populations were isolated in a series of small and discrete subterranean basins where genetic drift led to the evolution of separate species from the original founder population.

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References

- Barnard, J.L., and Williams, W.D., 1995. The taxonomy of Amphipoda (Crustacea) from Australian fresh waters. Part 2. *Records of the Australian Museum* 47(2): 161–201.
- Barr, T.C., and Holsinger, J.R., 1985. Speciation in cave faunas. *Annual Review of Ecology and Systematics* 16: 313–337.
- Bradbury, J.H., and Williams, W.D., 1995. A new genus and species of crangonyctoid amphipod, (Crustacea) from Western Australian fresh waters. *Transactions of the Royal Society of South Australia* 119(2): 67–74.
- Bradbury, J.H., and Williams, W.D., 1996a. Freshwater amphipods from Barrow Island, Western Australia. *Records of the Australian Museum* 48: 33–74.
- Bradbury, J.H. and Williams, W.D., 1996b. Two new species of anchialine amphipods (Crustacea, Hadziidae, *Liagoceradocus*) from Barrow Island, Western Australia. *Records of the Western Australian Museum* 17(4) in press.
- Comin, F. and Williams, W.D., 1994. Parched continents: our common future? Pp 473–527 in: Margalef, R. (ed.), *Limnology now; a paradigm of planetary problems*. Elsevier: Amsterdam.
- Culver, D.C., 1982. *Cave life. Evolution and ecology*. Harvard University Press: Cambridge, Mass.
- Eberhard, S.M., Richardson, A.M.M. and Swain, R., 1991. *The invertebrate cave fauna of Tasmania*. Department of Zoology, University of Tasmania: Hobart.
- Frey, D.G., 1991. A new genus of alonine chydorid cladocerans from athalassic saline waters of New South Wales, Australia. *Hydrobiologia* 224: 11–48.
- Holsinger, J.R., 1991. What can vicariance biogeographic models tell us about the distributional history of subterranean amphipods? *Hydrobiologia* 223: 43–45.
- Holsinger, J.R., 1993. Biodiversity of subterranean amphipod crustaceans: global patterns and zoogeographic implications. *Journal of Natural History* 27: 821–835.
- Holsinger, J.R., 1994a. Pattern and process in the biogeography of subterranean amphipods. *Hydrobiologia* 287: 131–145.
- Holsinger, J.R., 1994b. Amphipoda. Pp. 147–163 in: Juberthie, C. and Decou, V. (eds), *Encyclopaedia Biospeologica* 1: Société de Biospéologie.
- Humphreys, W.F., 1995. Limestone of the east Kimberly, Western Australia — karst and cave fauna. *Report to the Australian Heritage Commission and to the Western Australian Heritage Committee*. 190+ xix pp. Unpublished.
- Jennings, J.N., 1985. *Karst geomorphology*. Blackwell: Oxford.
- Knott, B., 1983. Amphipods from Nurina Cave — Nullabor Plain. *Australian Speleological Federation Newsletter* 101: 3–4.
- Knott, B., 1985. Australian aquatic cavernicolous amphipods. *Paper presented to the 15th biennial conference, Australian Speleological Federation, Hobart*. 11 pp.
- Mathews, P.G. (ed.), 1985. *Australian karst index*. Australian Speleological Federation Inc.: Melbourne.
- Paine, A.G.L. (ed.), 1990. *Australia. Evolution of a continent*. Australian Government Publishing Service: Canberra.
- Timms, B.V., 1993. Saline lakes of the Paroo, inland New South Wales, Australia. *Hydrobiologia* 267: 269–289.
- Williams, W.D., 1964. Subterranean freshwater prawns in Australia (Crustacea: Decapoda:

- Atyidae). *Australian Journal of Marine and Freshwater Research* 15(1): 93–106.
- Williams, W.D., 1986. Amphipoda on land masses derived from Gondwana. Pp. 551–559 in: Botosaneanu, L. (ed.), *Stygofauna Mundi*. Brill and Backhuys: Leiden.
- Williams, W.D. and Barnard, J.L., 1988. The taxonomy of crangonyctoid Amphipoda (Crustacea) from Australian fresh waters: foundation studies. *Records of the Australian Museum, Supplement* 10: 1–180.

TRANSLITTORAL TALITRIDAE (CRUSTACEA: AMPHIPODA) AND THE NEED TO RESERVE TRANSITIONAL HABITATS: EXAMPLES FROM TASMANIAN SALTMARSHES AND OTHER COASTAL SITES

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Abstract

Richardson, A.M.M., Swain, R. and Wong, V., 1997. Translittoral Talitridae (Crustacea: Amphipoda) and the need to reserve transitional habitats: examples from Tasmanian saltmarshes and other coastal sites. *Memoirs of the Museum of Victoria* 56(2): 521-529.

Transitional habitats, e.g., those that lie between sea and land, are often ignored because of the different backgrounds of marine and terrestrial biologists, but they are important for the series of species which span the boundary. The amphipod family Talitridae has perhaps the widest translittoral range and so provides evidence from which the evolutionary process of land colonisation can be deduced. The talitrids found on two sea-land transitions in Tasmania, a sandy-beach to rainforest and a saltmarsh to dry woodland, are described, and the significance of their distributions is discussed. The need to reserve the full range of such translittoral series is noted. This will not necessarily be achieved by establishing reserve boundaries on the basis of vegetation associations.

Introduction

Transitional habitats, that is those lying between major habitats (land and sea, freshwater and land) tend to fall through the net of biological investigations (Little, 1990). Marine biologists and terrestrial biologists develop from such different backgrounds that they have little to do with each other and so the zones of interaction between their spheres of operation tend to be ignored. While marine biologists often work in the intertidal zone, their studies tend to be concentrated well below the high water mark, while few terrestrial biologists approach the high water mark from the other direction. Thus the amount of study on the intermediate zone is small, and this is particularly obvious when the transitional zone is extensive, as it is in the most sheltered sea-land interfaces, in saltmarshes and mangroves.

And yet the interface between the two major habitats is in many ways more important than the sea or land alone. The colonisation of land was one of the greatest evolutionary events in the history of those seven phyla that have achieved terrestriality. Although most of the colonisation events happened a long time ago, the habitats in which they occurred are still there, and in some cases species can be found filling many of the intermediate stages. In a few taxa, which might be called translittoral (Chester, 1992), series of species can be found with distributions spanning the entire range from fully

marine to fully terrestrial. The best examples are the amphipod crustacean family Talitridae and the pulmonate mollusc family Ellobiidae. Translittoral groups of this type provide very valuable opportunities to reconstruct the evolutionary events leading to life on land (Little, 1989, 1990), and they become more valuable still when the species involved are relatively closely-related, as in the two families mentioned above.

In this contribution we will present evidence of translittoral distributions in the Talitridae and demonstrate that such distributions require a broader approach to reserve design than has been adopted hitherto.

Talitridae

The Talitridae include the only fully terrestrial members of the Amphipoda, one of only two crustacean groups (the other is the Isopoda) which have members that are fully terrestrial, i.e. independent of free water for all of their life stages. The Talitridae have been loosely classified by Bousfield (1984) into four groups, the palustral talitrids (marsh-hoppers), the beach-fleas, the sandhoppers and the landhoppers. The marsh-hoppers include the most plesiomorphic forms and they are found in the lower levels of saltmarshes and mangroves, where they have an amphibious lifestyle, entering and swimming efficiently in seawater even at low tide. In some places (Tasmania: Chester, 1992, South Africa:

Griffiths, 1976) their distributions extend into fully freshwater streams. In south east Australia the genus *Eorchestia* is widespread in salt-marshes and the lower reaches of associated streams (Richardson, 1993). The beachfleas and sandhoppers are the typical talitrids of the intertidal zone, distinguished by the adaptations of sandhoppers for their particular habitat, i.e. loose sand. Thus the sandhoppers are large, robust and spiny talitrids, sometimes with unusual morphological adaptations for life in sand. They are efficient burrowers. The beachfleas, in contrast, are not well-developed for burrowing, preferring to seek refuge under cast seaweed or stones (non substrate modifiers: Macintyre, 1963, or nestlers: Griffiths, 1976); they are generally more lightly built and weakly spined. Beachfleas are usually found on rocky or muddy shores, but there is at least one undescribed species in Tasmania which has become convergent with the sandhoppers and forages on mid-tidal wet sand during low tide, taking refuge in a shallow burrow during high tide.

The landhoppers are found in a range of terrestrial habitats in the Southern Hemisphere, Japan, the Phillipines, Central America, the Caribbean and many oceanic islands. In Tasmania they are found throughout the island, but where they have colonised continents (Australia, southern Africa) they are confined to the higher rainfall zones around the continental margins. Bousfield (1984) recognises two subgroups, the plesiomorphic simplidactylate genera, which seem to be descended from a marsh-hopper like ancestor, and the cuspidactylate genera which apparently arose from the beachfleas. The simplidactylate forms are confined to Australia and southern Africa.

Thus the Talitridae show a truly translittoral range from the semi-aquatic marsh-hoppers to the landhoppers. The sister family to the Talitridae is the Hyalidae, and it is widely-accepted that talitrids descended from a hyalid-like ancestor (Bousfield, 1984). Aquatic hyalids may be found adjacent to intertidal talitrids in fully marine and brackish waters, providing a valid extension to the translittoral series.

It seems likely that the talitrid amphipods colonised land relatively recently compared to other terrestrial arthropods. Little (1990) noted that the fossil record of the amphipods is only from the Quaternary, but Bousfield (1984) and Bousfield and Poinar (1995) suggests a mid-Cretaceous origin for the simplidactylate landhoppers of the Southern Hemisphere conti-

nents, contemporary with an extensive radiation of the angiosperm flora in Gondwana.

Tasmania has a remarkably rich talitrid fauna (Richardson, 1993, 1996) which includes representatives of all Bousfield's groupings. The taxonomy of the landhoppers is well-known (Friend, 1987) and the diverse intertidal fauna is currently being described by the senior author. Friend (1987) divided the Tasmanian landhopper fauna into three ecological groupings, one of which he called the coastal group. Five or six species in three genera make up this group and they have distributions which are strongly restricted to a narrow zone, less than 100 m wide, immediately behind the high tide mark.

Tasmania also retains some places, especially in the west, where transitions from land to sea remain undisturbed, and clothed with native vegetation. These provide important opportunities to study the natural distributions of talitrid amphipods, isopods and other groups across the transition. We will consider two cases, a sandy beach to wet sclerophyll forest at South Cape Bay and a saltmarsh to dry woodland transition at Lutregala Marsh on Bruny Island. Details of these studies are described elsewhere (South Cape Bay: Richardson et al., 1991; Lutregala Marsh: Richardson and Mulcahy, in press).

Study areas and methods

South Cape Bay

South Cape Bay is in the extreme south of Tasmania (Fig 1). It faces almost due south, but is sheltered from the prevailing south westerly and westerly winds by promontories to the west. Because of strong wave action, the sand above the highwater mark is colonised by few foredune plants, so that low coastal scrub and forest appears within a few metres of high water. Closest to the shore the shrubs *Correa backhousiana*, *Cyathodes abietina*, *Westringia brevifolia* and *Olearia phlogopappa* form a low dense cover, five to ten metres deep, which gives way to low forest with emergent trees of *Eucalyptus nitida*, sassafras, *Atherosperma moschatum*, celery top pine, *Phyllocladus aspleniifolius*, and southern beech, *Nothofagus cunninghamii*. This coastal forest has an understorey of native laurel, *Anopterus glandulosus*, and often cutting grass, *Gahnia grandis*. The ground layer is mostly absent, apart from a few mosses and herbs. The vegetation becomes lower and more wind-pruned from the western to the eastern end of the bay.

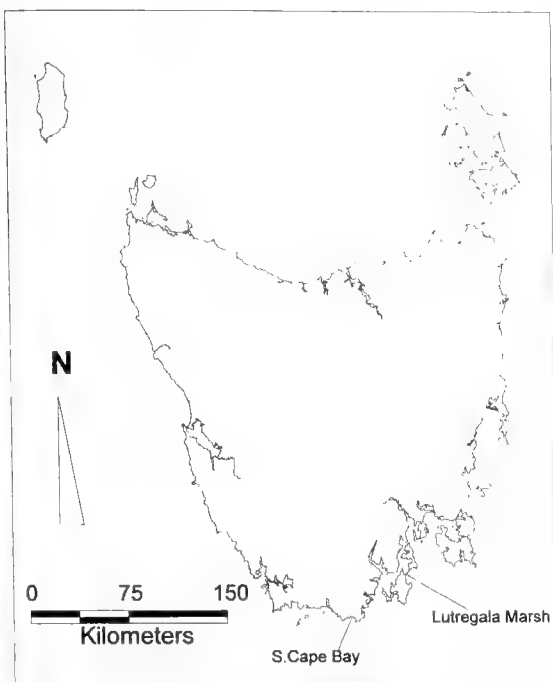


Figure 1. Tasmania, showing the locations of the two study sites mentioned in the text.

The topography immediately inland from the beach consists of a series of two or three low ridges, apparently stabilised dunes, separated by damper swales. The most landward ridge becomes higher from west to east, but at the eastern end of the bay erosion has cut into these structures, eliminating the lower seaward ridges and forming a sand cliff approximately 8 metres high. The soils are sandy, but at the eastern end of the bay waterlogged clayey soils appear within 30 m inland of the top of the sand cliff.

Two transect lines were set up in February 1989, at right angles to the high water mark, from below the extreme high water mark of spring tides (EHWS) to between 40 and 70 m inland. At each meter mark along these transects a pitfall trap was set. The traps consisted of a plastic container of 5 cm diameter and 10 cm depth, let into the soil so that the lip of the trap was flush with the surface of the sand, soil or leaf litter. Saturated picric acid solution (5–10 ml) was placed in the traps as a non-volatile preservative and Petri dish lids were supported on twigs over the traps to prevent rainwater from entering them. Traps were set for one series of ten nights in February and another of 14 days in July 1989.

Lutregala Marsh

Lutregala Marsh is situated on the west coast of Bruny Island, which is just off the south east coast of Tasmania (Fig. 1). The marsh has a diverse talitrid fauna, and, importantly, a relatively undisturbed transition from saltbush salt-marsh through saline tussock grassland to native terrestrial vegetation, despite some grazing by cattle on the higher levels. The marsh occupies approximately 10 ha.

Two sampling methods were employed to determine the distribution of amphipods. Firstly, two transects of pitfall traps, more or less at right angles to the high water mark, were placed across the marsh, and extended into terrestrial vegetation up to 50 m beyond the extreme high water mark. Pitfalls were constructed in the same way as at South Cape Bay. Transect A was set and retrieved three times between March and October 1990 during overnight low spring tides, but Transect B was only used once because of persistent flooding.

In the second approach to sampling, collections were made extensively over the marsh. From a recent, colour aerial photograph, collection sites were chosen that could easily be identified on the ground, and which represented the range of vegetation types present. At each sampling site, at least 20 amphipods were collected with an aspirator, and the same environmental variables that were collected at each pitfall site were measured. These collections were also made between March and October 1990. This period covers both the non-breeding (winter) and early breeding season of the species present.

Results

South Cape Bay

Twelve species, three of which were supralittoral sandhoppers, are listed in Table 1. Two undescribed species of *Tasmanorchestia* Friend were identified, and none of the sandhoppers has been placed in a specific taxon because of the poor taxonomic knowledge of this group.

The catches from the pitfall traps (Figure 2a-d) show distinct zonations in the distribution of species. Among the sandhoppers, there is a clear series, with 'Talorchestia' species 1 found closest to the sea, followed by 'Talorchestia' species 2, which in turn is replaced by 'Talorchestia' species 3. The replacement of sandhoppers ('Talorchestia' species 3) by landhoppers (*Austrotroides maritimus* Friend) is very sharp. The overlap was never more than 2 traps (= 2 m), and on several nights there was no overlap at all.

Table 1. Talitrid amphipods collected at South Cape Bay and Lutregala Marsh, with their phylogenetic affinities, ecological groupings and abundance. Bousfield's (1984) groupings are as follows. I:i: palustral talitrids. II:iii: cuspidactylate beachfleas having a 4-dentate lacinia mobilis on the left mandible. III:i: sandhoppers having a 4-dentate lacinia mobilis on the left mandible; III:ii: sandhoppers having a 5-dentate lacinia mobilis on the left mandible. IV:i: simplidactylate landhoppers. IV:ii: cuspidactylate landhoppers.

Taxon	Bousfield Group (Bousfield 1984)	Landhopper Ecological Group (Friend 1987)	Abundance at South Cape Bay	Abundance at Lutregala
<i>Eorchestia palustris</i> Richardson	I:i		—	Common
Beachflea	II:iii		—	Common
<i>Talorchestia</i> sp. 3	III:i		Common	—
<i>Talorchestia</i> sp.1	III:ii		Common	—
<i>Talorchestia</i> sp. 2	III:ii		Common	—
<i>Austrotroides maritimus</i> Friend	IV:i	Coastal	Common	Common
<i>A. longicornis</i> Friend	IV:i	Western forest	Rare	—
<i>Keratroides rex</i> Friend	IV:i	Coastal	Scarce	Scarce
<i>Mysticotalitrus tasmaniae</i> (Ruffo)	IV:i	Eastern forest	Common	Common
<i>M. cryptus</i> Friend	IV:i	Eastern forest	Scarce	Scarce
<i>K. vulgaris</i> (Friend)	IV:i	Eastern forest	Common	Scarce
<i>K. angulosus</i> (Friend)	IV:i	Eastern forest	Common	—
<i>Neorchestia plicibrancha</i> Friend	IV:i	Western forest	Common	—
<i>Tasmanorchestia</i> Friend sp.1	IV:ii	Coastal	Rare	—
<i>Tasmanorchestia</i> Friend sp.2	IV:ii	Coastal	Rare	Rare

On transect A there was a complete replacement of sandhoppers by *A. maritimus* from trap 9 to trap 10, with no sandhoppers in trap 10 and no *A. maritimus* in trap 9 after 14 nights of catching. Once beyond the landward range of the sandhoppers, the catch at S. Cape was dominated by *A. maritimus* for the next 20–30 m inland. *Tasmanorchestia* sp. and *Keratroides rex* also appeared, but in very low numbers, and only on transect B in the summer series.

Samples collected by hand, during the day, (Table 2) from the four swales on S. Cape Bay transect B did not contain the same proportions of species as the pitfall traps at all sites. At the seaward end, hand samples failed to catch sandhoppers but caught a much higher number of *A. maritimus* and *K. vulgaris*. Further landward, most species were much less likely to be trapped than caught by hand, and only *A. maritimus* and *M. tasmaniae* were over-represented in the traps.

Further inland, beyond the traplines, the landhopper community in forest litter changes, with no trace of the coastal group species or *Mysticotalitrus tasmaniae*. *K. angulosus* and *Neorchestia plicibrancha* become the dominants, with *Austrotroides longicornis* Friend appearing at a

drier site about 1 km from the beach. Further inland still, *N. plicibrancha* was the only species collected in rainforest several kilometers from the coast.

Lutregala Marsh

Eight species of talitrid amphipods were identified at Lutregala Marsh. These included one species from each of the palustral and beachflea groups, three coastal species and three forest species (Table 3). One of the coastal species was an apparently undescribed species of *Tasmanorchestia* Friend.

Profiles of the transects, the distributions of amphipods and the levels of the environmental parameters are shown in Figs 3a and 3b. Both transects cross a slight rise at their seaward ends, but Transect B is clearly much lower than Transect A and liable to tidal flooding over most of its length. At their landward ends both transects rise slightly and pass into terrestrial vegetation. The most striking contrast in the amphipod fauna is the absence of *Eorchestia palustris* on the drier Transect A, where it is replaced in the lower sites by the beachflea. On Transect B the beachflea is mostly confined to the upper levels of the transect, beyond the range of *E. palustris*.

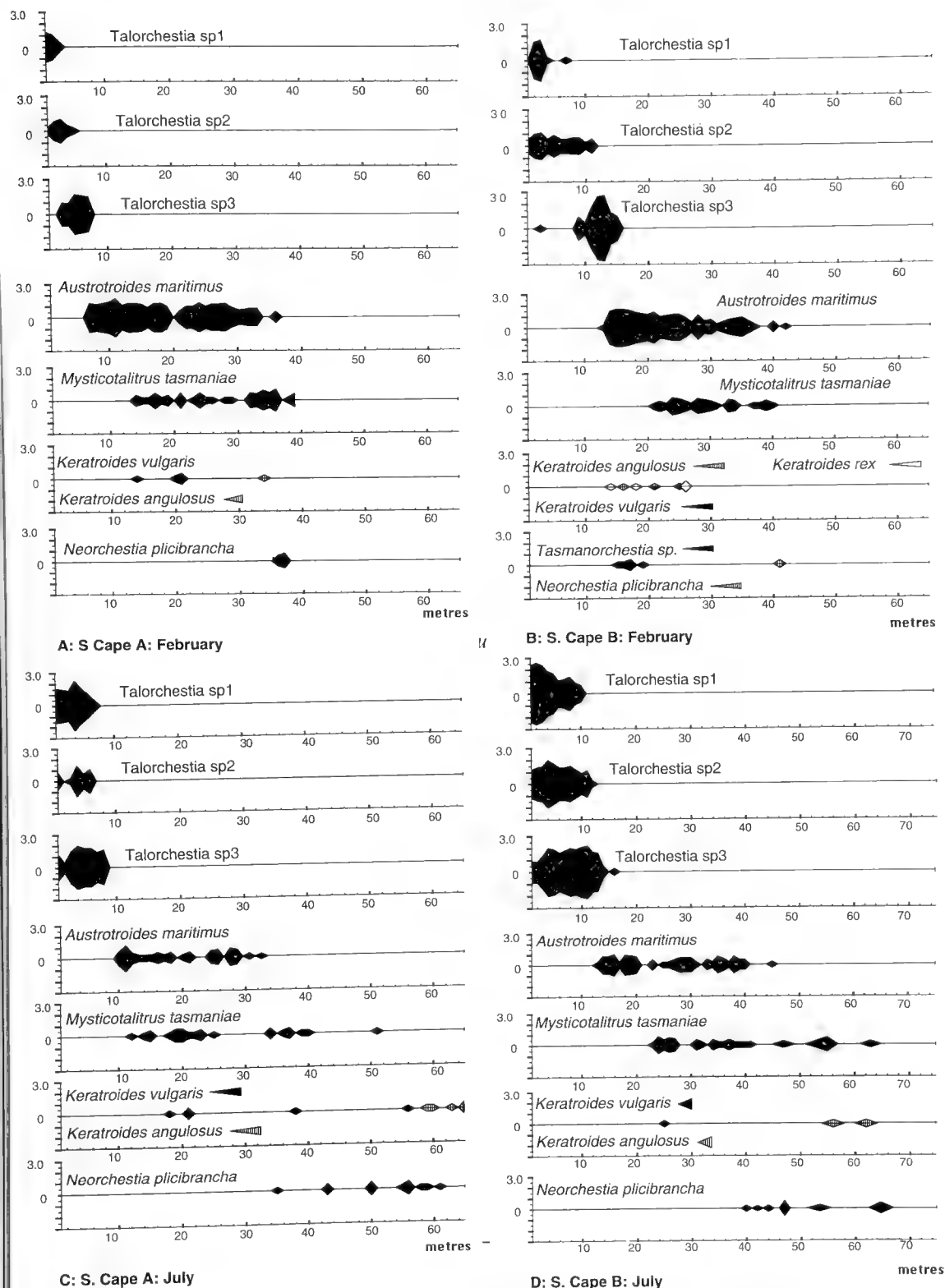


Figure 2a-d. Catches of talitrid amphipods in pitfall traps at South Cape Bay, Tasmania. The horizontal axis is in metres from Trap 1 which was set at the seaward edge of the strandline vegetation; the vertical axis is $\log_{10}(X + 1)$, where X is the average daily catch of each species in each pitfall. The transects extended 40 m (A) or 45 m (B) inland during the February series, but were extended to 70 m in the July series.

Table 2. Catches of talitrid amphipods by hand (first figure) or pitfall (second figure) at or near South Cape Bay (no pitfalls were set inland of the 4th swale). Species abbreviations are as follows. Tal 2: *Talorchestia* sp. 2; Tal 3: *Talorchestia* sp. 3; Austr mar: *Austrotroides maritimus*; Kera vulg: *Keratroides vulgaris*; Kera angu: *Keratroides angulosus*; Myst tas: *Mysticotalitrus tasmaniae*; Myst cryp: *Mysticotalitrus cryptus*; Neor plic: *Neorchestia plicibranchia*; Austr long: *Austrotroides longicornis*.

	Tal 2	Tal 3	Austr mar	Kera vulg	Kera angu	Myst tas	Myst cryp	Neor plic	Austr long
Swale 1	0/1	3/96	125/1	20/0	—	—	—	—	—
Swale 2	—	0/3	125/4	78/0	6/0	30/0	—	3/0	—
Swale 3	—	—	2/4	128/1	11/0	9/8	—	8/0	—
Swale 4	—	—	—	40/0	75/2	4/4	—	35/6	—
70 m	—	—	—	1	14	—	—	6	—
1 km	—	—	—	—	—	—	14	14	6
5 km	—	—	—	—	—	—	—	8	—

On both transects there is considerable overlap between the distributions of the beachflea, coastal landhoppers, and forest landhoppers.

Fig 4 shows the distribution of species from the four ecological groups of amphipods that were present (marsh-hoppers, beachfleas, coastal and forest landhoppers) over the marsh and the major vegetation types. *Eorchestia palustris* is restricted to the wet marsh vegetation where it is regularly inundated, while the beachflea extends more deeply into the upper marsh and terrestrial vegetation. The forest landhoppers are restricted to the terrestrial scrub, but the coastal landhoppers are found both there and in the upper marsh.

Discussion

At South Cape Bay the interface between the beach and the adjacent forest is quite sharp. There was complete replacement of sandhoppers by landhoppers within 4 metres, at the point where woody vegetation formed a closed canopy and substantial amounts of organic matter began to appear in the sandy soil. The coastal landhoppers extend inland for another 50 m, beyond which the landhopper community becomes much less diverse than in the coastal zone. Further work at South Cape Bay and elsewhere in the west of Tasmania (Richardson, 1993, in prep.) shows that the distance that the coastal species penetrate inland is related to exposure to wind, perhaps because this increases the amount of salt spray deposited behind the shore.

At Lutregala Marsh, in contrast, there is no obvious point where intertidal talitrids (in this

case beachfleas) are replaced by landhoppers, since there are substantial overlaps both between the distributions of the beachflea and the coastal landhoppers and between the beachflea and the marsh-hoppers which occupy a zone closer to the sea.

The numbers of talitrid species present at both sites is high, 11 species at South Cape Bay and eight at Lutregala Marsh, and phylogenetically diverse. Although the phylogeny of the Talitridae is not clearly understood, it is generally accepted (Bousfield, 1984, Moore et al., 1993) that sandhoppers form a distinct, specialised group that is unlikely to have produced any forms ancestral to the landhoppers. This, combined with the absence of beachfleas and the abrupt transition from beach fauna to forest fauna, suggests that sandy beaches were unlikely to have been the site where the colonisation of land by talitrids began. On the saltmarshes, both of the likely ancestral groups are present (marsh-hoppers and beachfleas), the transition to land is gradual, distributions overlap substantially and the saltmarsh habitat foreshadows land in the structure and nutritional nature of its vegetation.

In both these examples there are reasons why the phenomena of interest cover a wider range than "shore" or "land", however they might be defined. Certainly vegetation patterns do not give any indication of the inland limits of coastal landhoppers in either location. There has been some interest in the reservation of saltmarsh vegetation in Tasmania (Kirkpatrick & Glasby 1981), but by definition that has referred to salt-marsh plants. There are many records of beach-

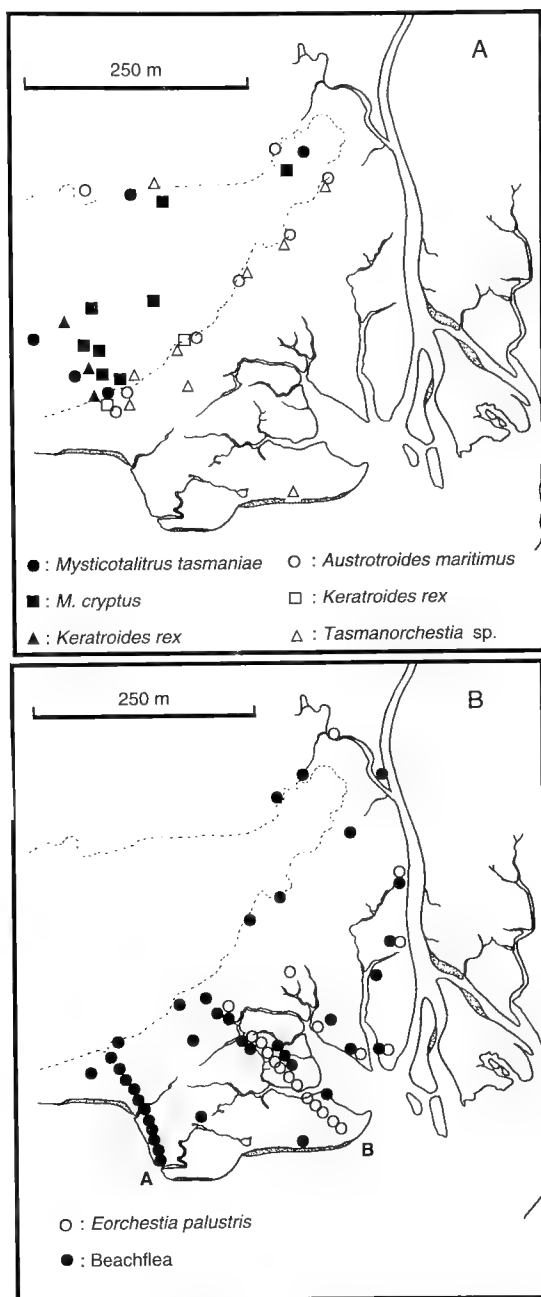
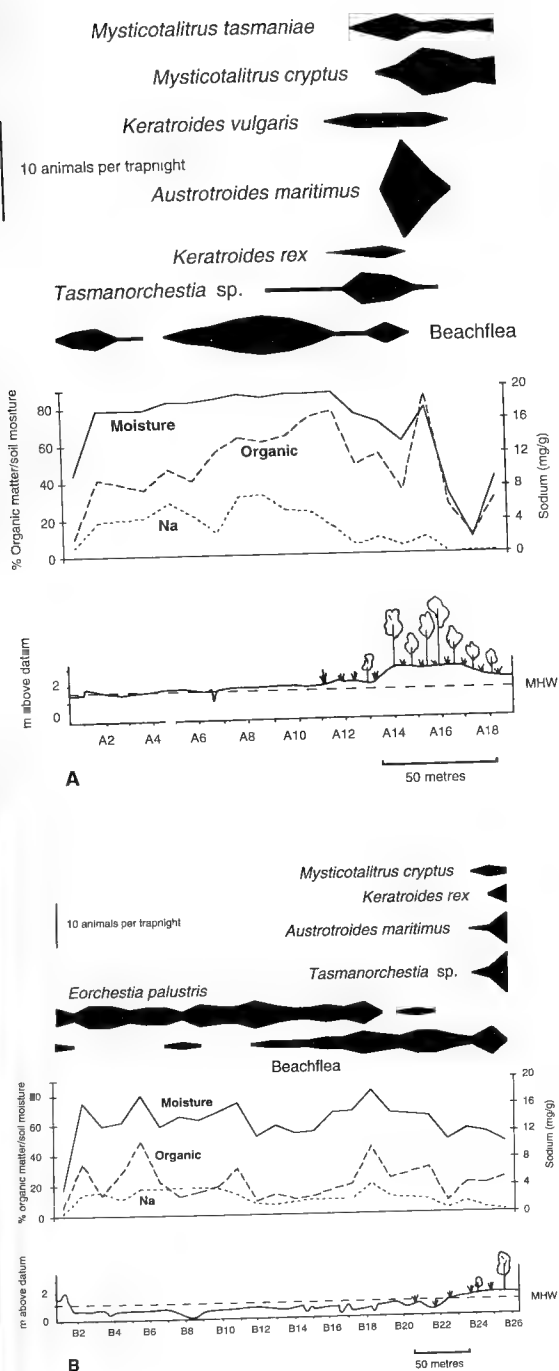


Figure 4a, b. Maps of Lutregala Marsh, showing the distributions of the four ecological groups of talitrid amphipods. A: marsh-hoppers and beachfleas; B: coastal and forest landhoppers. The dashed line represents the approximate boundary of woodland. Samples were collected by hand, and from the pitfall transects (A: start of transect A; B: start of transect B). Filled symbols refer to species of the forest landhopper group, or the beachflea, open symbols to the coastal landhopper group or to the palustral group (*Eorchestia palustris*).

Figure 3a, b. Profile of two transects on Lutregala Marsh, showing the levels of soil moisture, soil organic content and soil salinity at each trapping position, and the relative abundance of amphipods trapped in pit-falls. MHW: mean high water level.

fleas extending their range into terrestrial vegetation, usually in situations where there is considerable salt spray (eg Reid 1947, Bagenal 1957, Kuhnelt 1976, Bousfield 1982), and the coastal landhoppers, which are part of the translittoral series, extend beyond the landward limit of the recognised saltmarsh plants.

In a survey of the crustacean and mollusc fauna of Tasmanian saltmarshes, Wong et al. (1993) recorded the factors causing disturbance at 52 saltmarshes and 11 other brackish marshes around the Tasmanian coast. As well as grazing, invasion by exotic species, landfill, catchment modification, fire and off-road vehicles, all noted by Kirkpatrick and Glasby (1981), they also recorded the condition of the vegetation immediately behind the marshes. Very few of the marshes retained intact backing vegetation, since land clearance for grazing behind the marshes is very common (indeed, grazing in the marshes is one of the most common disturbance factors). Wong et al. (1993) recommended nine marshes for listing on the Register of the National Estate and added another three marshes of high conservation value, but even amongst this group, only five were recorded as having intact backing vegetation. Thus while it may be relatively easy to select saltmarshes for reservation on the basis of values within the marsh as defined by the vegetation, there are very few opportunities to reserve the complete series of distributions of the translittoral talitrids.

Fortunately, the situation with sandy beaches and their backing vegetation is not so bad, at least in the western half of the island, where much of the coast lies within the Western Tasmania World Heritage Area. Elsewhere, in lower rainfall areas the dunes that back the beaches are often colonised by the introduced marram grass, *Ammophila arenaria*, but in another survey (Richardson et al., in prep.), a few beaches on the east coast have been identified where the coastal vegetation remains undisturbed.

It is regrettable, though pragmatic, that reservation decisions so often have to be made on the basis of vegetation patterns, without any reference to animal distributions. While it is not surprising that there is often no clear correlation between animal distributions and plant associations, in some cases, such as the translittoral groups discussed here, defining reserves in vegetational terms can lead to the failure to protect significant zoological phenomena. There is considerable interest in the ecophysiology of land colonisation in talitrid amphipods (c.g., Moore

et al., 1993, Morritt, 1987, 1988, 1989; Spicer et al., 1987; Spicer and Taylor, 1987, 1994), and Tasmania provides perhaps the best opportunity in the world to combine ecophysiology with studies of distributions and other aspects of the biology of a translittoral series, provided that places where that can be done remain intact.

Acknowledgements

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References

- Bagenal, T. B., 1957. The vertical range of some littoral animals on St. Kilda. *Scottish Naturalist* 69: 50–51.
- Bousfield, E.L., 1982. The amphipod superfamily Talitroidea in the Northeastern Pacific region. 1. Family Talitridae: systematics and distributional ecology. *National Museums of Natural Science, Ottawa, Publications in Biological Oceanography* 11: 1–73.
- Bousfield, E.L., 1984. Recent advances in the systematics and biogeography of landhoppers (Amphipoda: Talitridae) of the Indo-Pacific region. Pp. 171–210 in: Radovsky F.J., Raven, P.H. and Sohmer, S.H. (eds), *Biogeography of the tropical Pacific*. Association of Systematic Collections and the Bernice P. Bishop Museum: Honolulu.
- Bousfield, E.L. and Poinar, G.O.J., 1995. New terrestrial amphipod from Tertiary amber deposits of the Dominican Republic. *Journal of Crustacean Biology* 15: 746–755.
- Chester, E.T., 1992. *The life history of the palustral talitrid Eorchestia palustris (Crustacea: Amphipoda: Talitridae)*. Unpublished Honours thesis, University of Tasmania. 165 pp.
- Friend, J.A., 1987. The terrestrial amphipods (Amphipoda: Talitridae) of Tasmania: systematics and zoogeography. *Records of the Australian Museum, Supplement* 7: 1–85.
- Griffiths, C.L., 1976. *Guide to the benthic marine amphipods of southern Africa*. South African Museum: Cape Town. 106 pp.
- Kirkpatrick, J.B. and Glasby, J., 1981. *Saltmarshes in Tasmania*. Occasional Paper Number 8, Department of Geography, University of Tasmania. 62 pp.
- Kuhnelt, K., 1976. *Soil biology with special reference to the Animal Kingdom*. Faber and Faber: London. 483 pp.

- Little, C., 1989. Comparative physiology as a tool for investigating the evolutionary routes of animals onto land. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 80: 201–208.
- Little, C., 1990. *The terrestrial invasion*. Cambridge University Press: Cambridge. 304 pp.
- Moore, P.G., Morritt, D. and Stevenson, T.D.I., 1993. Morphology of the antennary gland exit duct in ecological and phylogenetic series of talitroid Amphipoda (Crustacea). *Journal of Zoology* 231: 187–201.
- Morritt, D., 1987. Evaporative water loss under desiccation stress in semiterrestrial and terrestrial amphipods (Crustacea: Amphipoda: Talitridae). *Journal of Experimental Marine Biology and Ecology* 111: 145–157.
- Morritt, D., 1988. Osmoregulation in littoral and terrestrial talitroidean amphipods (Crustacea) from Britain., *Journal of Experimental Marine Biology and Ecology* 123: 77–94.
- Morritt, D., 1989. Ionic regulation in littoral and terrestrial amphipods (Crustacea: Amphipoda: Talitridae), *Journal of Experimental Marine Biology and Ecology* 132: 53–67.
- Reid, D.M., 1947. Talitridae (Crustacea Amphipoda). *Linnaean Society Synopses of the British Fauna* 7: 1–25.
- Richardson, A.M.M., 1993. The distribution of coastal landhoppers (Crustacea: Amphipoda: Talitridae) related to sea spray at Cox Bight, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 127: 55–60.
- Richardson, A.M.M., 1996. A new species of *Protorchestia* Bousfield (Crustacea: Amphipoda: Talitridae) from Maatsuyker Island, Tasmania, with a key to the genus and notes on the diversity of Tasmanian Talitridae. *Journal of Crustacean Biology* 16: 574–583.
- Richardson, A.M.M. and Mulcahy, M.E., in press. The distribution of talitrid amphipods (Crustacea) on a saltmarsh in southern Tasmania, in relation to vegetation and substrate. *Estuarine, Coastal and Shelf Science*.
- Richardson, A.M.M., Swain, R. And Smith, S.J., 1991. Local distributions of sandhoppers and landhoppers (Crustacea: Amphipoda: Talitridae) in the coastal zone of western Tasmania. *Hydrobiologia* 223: 127–140.
- Richardson, A.M.M., Swain, R. and Shepherd, C. (in prep.) *A survey of the fauna of the upper regions of sandy beaches on the east coast of Tasmania*. Report to the National Estate Grants Program.
- Spicer, J.I. and Taylor, A.C., 1987. Respiration in air and water of some semi- and fully terrestrial amphipods (Crustacea: Amphipoda). *Journal of Experimental Marine Biology and Ecology* 106: 265–277.
- Spicer, J.I. and Taylor, A.C., 1994. The origin and metabolic significance of exosomatic water in the semi- terrestrial beachflea, *Orchestia gammarellus* (Crustacea: Amphipoda). *Journal of Zoology* 232, 617–632.
- Spicer, J.I., Moore, P.G. and Taylor, A.C., 1987. The physiological ecology of land invasion by the Talitridae (Crustacea: Amphipoda). *Proceedings of the Royal Society of London (Series B)*, 232: 95–124.
- Wong, V., Richardson, A. M. M. and Swain, R., 1993. *The crustaceans and molluscs of Tasmanian salt-marshes*. University of Tasmania: Hobart. Report to the National Estate Grants Program. 95 pp.

GONE TODAY, HERE TOMORROW — EXTINCT AQUATIC MACROINVERTEBRATES IN VICTORIA

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Abstract

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Only two aquatic macroinvertebrates have been given the official status of extinct (or presumed extinct) in Victoria. The Dandenong Amphipod *Austrogammarus australis* (Sayce) has been declared presumed extinct under the *Flora and Fauna Guarantee Act* 1988, the Department of Conservation and Natural Resources 1993 threatened fauna list and the Australian National Parks and Wildlife 1990 provisional list of threatened Crustacea species. The Otway Stonefly *Eusthenia nothofagi* Zwick was also listed under the *Flora and Fauna Guarantee Act* 1988 as presumed extinct in May 1991. A subsequent survey for amphipods in the Dandenong Ranges during 1995 has discovered specimens of *A. australis*, but with a very restricted distribution. Another survey, of eustheniid stoneflies in the Otways discovered that the species was common throughout the Otway Ranges. It is in the process of being de-listed. Now there are no officially extinct aquatic macroinvertebrates in Victoria. While this news should be greeted with joy by invertebrate biologists, it calls into question the current conservation status categories and processes when dealing with aquatic macroinvertebrates.

Introduction

As they (whoever they are) say, 'Extinction is forever'. Once extinct, a species cannot be resurrected, unless you believe in the outrageous popular myths propagated in films like 'Jurassic Park', and other fictional accounts of the activities of mad wild-haired scientists posing as biologists and ecologists. While a dictionary definition of the term 'extinct' corresponds with reality (i.e. the last individual of the species is dead), when it comes to more legal and bureaucratic official designations and conservation status lists, a slightly different tack is taken.

In conservation-speak, 'extinct' is generally defined as not having been recorded for a certain length of time. The IUCN (1983) and the CNR (1993) list of threatened Victorian fauna use a period of 50 years, although the CNR updated list (CNR 1995) uses 'taxa that are considered to have occurred in Victoria since European settlement but that have not definitely been recorded in the wild in Victoria in recent decades, and almost certainly no longer occur there'. Under the Victorian *Flora and Fauna Guarantee Act* 1988 (herein called the FFG Act), taxa can be listed as presumed extinct if they have not been recorded for 40 years.

While such conditions may be appropriate for

high profile groups with relatively few species that are investigated regularly by a number of searchers (e.g., mammals and birds) or some diverse, colourful or collectable groups of interest to a large number of people (e.g. butterflies), the use of the formal conservation term 'extinct' breaks down for groups that are rarely investigated, including many of the invertebrates.

In invertebrate biology, advances in our knowledge on the distribution, taxonomy and ecology of many invertebrate species are often made by individual workers who, for some reason best known to themselves, become interested or enthusiastic about a particular group of animals. After years of sampling, taxonomic and ecological studies, the individual moves on, leaving the group without a champion. No more studies are conducted with the oft repeated comment 'Oh, don't worry about it, that groups been done'. Quite often, after 40 or 50 years without any sampling, the group is suddenly suitable for declaration as extinct.

This paper presents the results of investigations of two previously presumed extinct taxa that, when someone takes the time and trouble to actually look for them, are raised from the dead.

Dandenong Amphipod
***Austrogammarus australis* (Sayce)**

Austrogammarus australis (Crustacea: Parameletidae) was originally described as *Gammarus australis* by Sayce in 1901 but placed in a new genus, *Austrogammarus*, erected by Barnard and Karman (1983), along with *Austrogammarus haasei* Sayce. The genus now includes seven species, four of which were first described by Williams and Barnard (1988) (*A. smithi*, *A. saycei*, *A. spinatus* and *A. multispinatus*) and another, *A. telsosetosus*, by Barnard and Williams (1995). *A. smithi* is known only from Tasmania, *A. telsosetosus* occurs only in South Australia, while the other species all appear to be restricted to Melbourne's eastern suburbs including sites around Monbulk, Sassafras, Croydon and Dandenong.

The type locality for *A. australis* was given as Dandenong Creek near Bayswater, but other locations where the species was subsequently located were given as the ambiguous 'a tributary of Monbulk Creek' and 'in a gully halfway to Sassafras'. The last known confirmed record of the species was in 1911. More recent attempts (Williams and Barnard 1988) to collect the species from the presumed type locality were unsuccessful, with the observation that the now modified urban drain nature of parts of Dandenong Creek near Bayswater made the location unsuitable for the species.

On the basis of the time since the last record, the failure to rediscover the species, and modifications to streams around the type locality, the species was classified as 'presumed extinct' by Horwitz (1990) and by the Department of Conservation and Natural Resources (CNR 1993). The species is also listed under the FFG Act as 'presumed extinct'.

In May and June 1995, a survey was conducted to try to confirm or deny the extinct status of the species. A total of 47 sites were surveyed throughout the Dandenong Ranges, and included sites within the Dandenong National Park and Olinda State Forest, as well as creeks from the suburbs of Heathmont, Bayswater, Ferntree Gully, Belgrave, Monbulk, Kallista, Kalorama, Lillydale, Mt Evelyn and Upway. These sites possibly included the type locality and the other original sites, but insufficient information is available to accurately locate these sites. At each site, samples were collected in likely habitats with an FBA net, placed in a sorting tray and all Amphipoda seen in the

sample during a period of 0.5 person hours were collected in the field.

A total of 409 individuals of Amphipoda were recorded from 31 out of 47 sites sampled (Fig. 1). All sites containing amphipods were located in the least disturbed higher altitude areas of the study area, with none found at sites in the lower more modified urban sections of streams. In terms of composition, by far the majority of the amphipod fauna of the Dandenong Ranges consisted of members of *Pseudomoera gabrieli* (Eusiridae — 91% of the individuals).

Using the key provided by Horwitz et al. (1995), individuals identified as *Austrogammarus* were located at ten sites (Fig. 1). *Austrogammarus australis*, as described by Williams and Barnard (1988), was recorded at nine of these sites. These were located in the three major catchments draining the Dandenong Ranges (Dandenong Creek, Monbulk Creek and Olinda Creek). Confirmation of the specimens' identity was provided by John Bradbury (University of Adelaide, pers. comm.). All sites were in the headwaters of streams, had generally low levels of modification, with predominantly native riparian vegetation and shaded stream sections, but there was no consistent trends that could be associated with particular in-stream characteristics.

Austrogammarus haasei was located at only two sites (26, 27 in Fig. 1), both in Sherbrooke Creek. At one site on Sherbrooke Creek (27), *A. haasei* was found co-existing with *A. australis*.

While *A. australis* is clearly not extinct, the designation of an alternative formal conservation category is difficult. Categories like Endangered and Vulnerable usually involve some demonstrable decline in abundance and/or range to some undetermined critical level, and some defined threat to their survival (CNR 1995). Such a decision cannot be made with certainty for this species. It has clearly declined in range (the type locality no longer exists) but to what extent is unknown, and whether the decline is continuing is unknown. What the critical level of abundance or distribution, below which it is certain to go extinct (in the real sense of the word) is unknown. Hence, it has been reclassified as Insufficiently Known (taxa suspected to be Rare, Vulnerable or Threatened — CNR 1995).

Of some significance is the situation regarding the other *Austrogammarus* species. Despite Williams and Barnard (1988) not listing any new records for *A. haasei* since the original descrip-

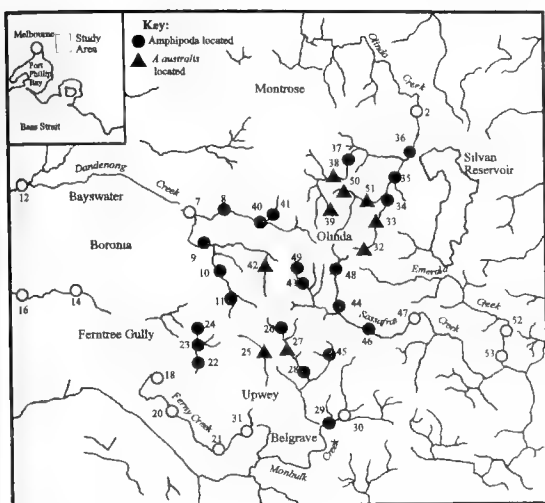


Figure 1. Map showing the distribution of Amphipoda in the Dandenong Ranges. Key: ? — Amphipoda recorded; 1 — *Austrogammarus australis* recorded.

tion (so, like the Dandenong amphipod, it could have been regarded as extinct prior to this study), it has never appeared on any threatened list (CNR 1993, Horwitz 1990). It has a distribution more restricted than *A. australis* and should probably have the same status or greater. How one species of *Austrogammarus* can appear on a formal list, while presumably the same publication used as key evidence also indicates that another species should be worthy of similar status, remains unexplained.

Otway stonefly *Eusthenia nothofagi* Zwick

The Otway stonefly, *Eusthenia nothofagi* Zwick, was described on the basis of differences in adult male genitalia from the other species in the genus, *E. venosa* (Tillyard), by Zwick (1979). This decision was based on adult male specimens from a single site held in the Museum of Victoria (collected in January 1932 from Beech Forest). However, without providing any definitive reason, Zwick stated that the two species (*E. venosa* and *E. nothofagi*) do not occur together. This has subsequently been taken to mean that *E. nothofagi* is restricted to the Otway Ranges, while *E. venosa* is widespread throughout the rest of Victoria. Until mid-1991, no additional confirmed records of the species had been noted.

On the basis of the presence of only a single confirmed location, *E. nothofagi* was listed as Endangered, ('taxa in danger of extinction and

whose survival is unlikely if the causal factors continue operating') by the International Union for Conservation of Nature and Natural Resources (IUCN 1983 — although note that the 50 years required for extinct status had just expired at the time of publication), and as Endangered by Department of Conservation and Natural Resources (CNR, 1993). The species was listed under the FFG Act in May 1991 as presumed extinct (40 year requirement).

However, in mid-1991, a male adult stonefly, subsequently identified as *E. nothofagi*, was collected by P. Lilywhite of the Museum of Victoria at Melba Gully State Park, near Lavers Hill. This was the first official record of the taxon since the original specimen from which the species description was made.

Again, a survey was conducted to determine the true distribution of the species. Fifty-two sites were sampled from across the Otway Ranges region, primarily within the forested areas, but extending outwards into the agricultural flats surrounding the ranges (Doeg and Reed 1995). At each site, a total of one person-hour was spent searching in the stream for *Eusthenia* nymphs. All habitat types within the stream (primarily wood debris and stones) were included. Possible habitat elements at each site were lifted and examined by eye for nymphs (this was possible due to the large size of the larvae).

Nymphs of the genus *Eusthenia* were recorded at 19 sites (Fig. 2). These were distributed over a wide area of the Otways, from the Johanna River (at Melba Gully State Park) and Chapple Creek (a tributary of the lower Gellibrand River) in the west, to the Erskine River at Erskine Falls in

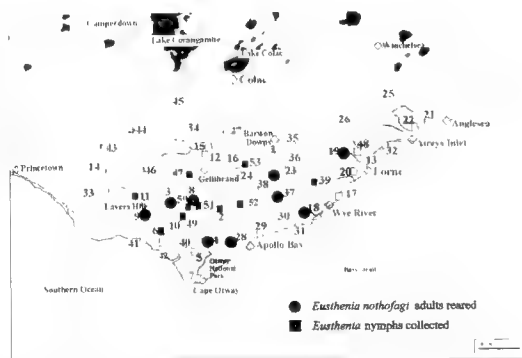


Figure 2. Map showing the distribution of the Otway stonefly in the Otway Ranges.

the east. Sites covered almost the entire range of altitudes found in the Otway Ranges (40–500m ASL). In the majority of cases, sites were located in forested areas (cool temperate rainforest, and wet sclerophyll forest), in State Forest or National Park. Two sites (the Ford and East Barham Rivers) were in areas where agricultural clearing was relatively extensive (although the specific sites were wide streams with abundant local riparian vegetation) and one (the Aire River at the Redwoods) was located primarily in pine forests.

Late instar nymphs were reared through to male *Eusthenia nothofagi* adults from 9 sites, confirming the presence of the species widely distributed throughout the Otway Ranges (Fig. 2). No adults of *Eusthenia venosa* were reared, and it is therefore assumed that, as suggested by Zwick (1979), all *Eusthenia* nymphs represent records for *Eusthenia nothofagi* and that the species is distributed at least from Melba Gully in the west, to Lorne in the east, a distance of some 50–60 km. It seems likely that the species would probably be located within virtually all the catchments between these extremes.

The presence in a large number of catchments, including reserved areas would suggest that the species is in little danger of becoming extinct. On the basis of these data, the species has been removed from the latest CNR threatened fauna list (CNR 1995) and is in the process of being delisted under the FFG Act (Pam Clunie, Flora and Fauna Branch, pers. comm.).

Conclusions

Formal conservation categories present difficulties when dealing with aquatic macroinvertebrates. With the current definitions, it is possible for species to be declared extinct while still thriving in reality. Other categories (Endangered and Vulnerable) require some demonstration of decline which, for many species, probably cannot be definitively established. The original suggestions that the Otway stonefly and the Dandenong amphipod were extinct are products of the lack of comprehensive surveys of each area, and complications in our taxonomic knowledge. Areas are rarely surveyed at the intensity seen in these two studies. Many studies only include a relatively small number of sites within a catchment. While a species with a restricted distribution (like *A. australis*) may be collected at one of these sites, this provides little information on the true distribution of the species. Such data sets will only increase the list

of taxa recorded from single sites (and hence suitable for formal conservation status listing). However, many other species with similar restricted distributions may also be missed.

The situation is complicated where taxonomic identification is based on adult features, when the most often collected forms are larvae or nymphs (hence the identity can only be guessed at, but not confirmed). Again, the lack of confirmed published records for these types of taxa will increase the number of species suitable for formal conservation status listing. While such problems are slowly being addressed through increased survey activity and improved taxonomic procedures, it is likely that many more taxa will come under scrutiny for inclusion in such lists (possibly as a product of the perceived conflict between preservation, conservation and development).

Such conflicts may lead to a 'stamp collecting' mentality approach to conservation status. It would be a simple matter to compile a list of invertebrate species described prior to 1945 (50 years ago), scan all the available published literature since then, and create a list of species that can be officially declared extinct. Species more recently described, but only recorded at, say, the type locality would also be eligible for listing as rare, or potentially threatened. Undoubtedly, such an approach would generate many taxa suitable for listing. But without an adequate knowledge of the survey effort put into the species, it will virtually impossible to designate the 'correct' conservation status for such species.

Only intensive further work will reveal that some of these easily nominated taxa considered rare are, in fact, common or secure. On the other hand, the number of taxa that will be shown to be rare or threatened will undoubtedly increase (Butcher and Doeg 1995), leading to the question of individual species management. The diversion of time, effort and money into confirming the status and developing management plans for all these potential species would be extensive, but may actually be of little or no value in the 'big picture' effort to conserve macroinvertebrate taxa. Yen and Butcher (1994) suggest that single species conservation may be inappropriate for the majority of invertebrates, but stress the importance of maintaining some type of list of threatened invertebrates because of the importance of listed species as flagship taxa.

Maybe it is time to examine our attitude to the setting of a formal conservation status for indi-

vidual invertebrate taxa. The formal definitions of conservation status categories are clearly inadequate, given the information available for the majority of species, so that any list produced will always be inadequate and sometimes incorrect. Even where distributions are well established, questions of historical decline or potential of extinction are often still unanswered. One option would be to automatically designate species believed to be worthy of conservation status into the Insufficiently Known category (taxa that are suspected but not definitely known to belong to other categories), until sufficient data to establish a realistic status is collected.

Another option may be to redefine the criteria under which invertebrate species are assigned to each formal category, taking into account the limitations of any data likely to be collected. A final approach may be to determine a system of 'confidence' measures, where species are assigned to the most likely category but is annotated with a measure of the strength of the data used to make the determination.

The problem is to devise a system where the values of a listing process are retained, and where truly rare invertebrate species, like *A. haasei*, are given their full recognition as important species. But a system is needed where the designation to a particular conservation status is defensible, according to sound recognised criteria, but also acknowledging the special nature of invertebrate data for many species.

As an adjunct to the listing process, a concerted effort to control the threatening processes that cause decline in invertebrate biodiversity is vital and may, in the long term, be a more appropriate and, a more successful approach to invertebrate conservation.

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References

- Barnard, J.L. and Karman, G.S., 1983. Australia as a major evolutionary centre for Amphipoda (Crustacea). *Memoirs of the Australian Museum* 18: 45-61.
- Barnard, J.L. and Williams, W.D., 1995. The taxonomy of Amphipoda (Crustacea) from Australian fresh waters: Part 2. *Records of the Australian Museum* 47: 161-201.
- Butcher, R. and Doeg, T., 1995. Conservation of freshwater invertebrates. *Victorian Naturalist* 112: 15-19.
- CNR, 1993. *Threatened fauna in Victoria*. Department of Conservation and Natural Resources: Victoria.
- CNR, 1995. *Threatened fauna in Victoria 1995*. Department of Conservation and Natural Resources: Victoria.
- Doeg, T. and Reed, J., 1995. Distribution of the endangered Otway stonefly *Eusthenia nothofagi* Zwick (Plecoptera: Eustheniidae) in the Otway Ranges. *Proceedings of the Royal Society of Victoria* 107: 45-50.
- Horwitz, P., 1990. *The conservation status of Australian freshwater crustacea*. Report No. 14. Australian National Parks and Wildlife Service: Canberra.
- Horwitz, P. Knott, B. and Williams, W.D. (1995) A (Crustacea) found in Australian inland waters. *Identification Guide No. 4*. Cooperative Research Centre for Freshwater Ecology: Albury.
- IUCN, 1983. *The IUCN invertebrate Red Data Book*. International Union for Conservation of Nature and Natural Resources: Switzerland.
- Williams, W.D. and Barnard, J.L., 1988. The taxonomy of crangonyctoid Amphipoda (Crustacea) from Australian freshwaters: foundation studies. *Records of the Australian Museum. Supplement*. 10: 1-180.
- Yen, A. and Butcher, R., 1994. *An overview of the conservation status of non-marine invertebrates in Australia*. Endangered Species Unit and Australian Nature Conservation Agency: Canberra.
- Zwick, P., 1979. Revision of the stonefly family Eustheniidae (Plecoptera), with emphasis on the fauna of the Australian region. *Aquatic Insects* 1: 17-50.

THE CONSERVATION STATUS OF DRAGONFLIES (ODONATA)
FROM SOUTH-EASTERN AUSTRALIA

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Abstract

Hawking, J.H., 1997. The conservation status of dragonflies (Odonata) from south-eastern Australia. *Memoirs of the Museum of Victoria* 56(2): 537-542.

The conservation status of the dragonflies from south-eastern Australia is documented and the species with limited distributions and/or larval habitats which are vulnerable are discussed. One hundred and seven species are recorded from South Australia, Victoria, Tasmania and southern New South Wales. No species is considered endangered, but nine species have high conservation priority. These species are endemic to Australia and all have restricted distributions. The vulnerability of the larval habitats is discussed and suggestions for their conservation and management are made.

Introduction

At present, 305 species of Odonata (damselflies and dragonflies) are known from Australia (Watson et al., 1991, Theischinger, pers. comm.). Of these, approximately 40% are endemic, and many can be considered as southern species, possibly Gondwanan relicts (Watson and O'Farrell, 1991). Most of the endemic species are uncommon, and restricted in distribution. These two factors suggest vulnerability to change and therefore their conservation status should be evaluated. In contrast, the non-endemics are generally common and have much wider distributions. For this reason the conservation of these species should not be ignored, but given a lower status.

The IUCN Invertebrate Red Data Book (Wells et al., 1983) listed the damselfly *Hemiphysalia mirabilis* Selys as endangered, the only Australian odonate so listed. Hill and Michaelis (1988) listed *Archipetalia auriculata* Tillyard and *Hemiphysalia mirabilis* as threatened and another 14 species (of which only *Austroaeschna hardyi* Tillyard and *Synthemiopsis gomphomacromioides* Tillyard occur in south-eastern Australia), which the late Dr J.A.L. Watson suggested were of significant conservation value.

Only limited attention has been given to the conservation of Australian Odonata, except for *Hemiphysalia mirabilis*. This paper attempts to evaluate the conservation status of the Odonata from south-eastern Australia, list the threatened species, identify the species habitats, list the threats to each species and suggest conservation

measures to be implemented. Conservation status of the odonate species is evaluated on the basis of the categories adopted from the IUCN Red Data Book by Hill and Michaelis (1988). The categories are:

- (a) Endangered species are in serious risk of disappearing within two decades if present causal factors continue;
- (b) Vulnerable species are endangered over a longer time or extremely localised and or patchy in distribution;
- (c) Rare species are not currently threatened but are extremely localised or patchy in distribution;
- (d) Indeterminate species are suspected of being threatened but too poorly known to assign to one of the preceding categories.

Species considered of conservation significance

Watson et al. (1991) recorded 107 odonate species from south-eastern Australia and from these nine (Table I) have been identified as worthy of conservation evaluation based on the rarity and restricted distribution.

Hemiphysaliidae *Hemiphysalia mirabilis* Selys

Hemiphysalia mirabilis was first positively recorded in the early 1900s from Alexandra, Victoria and has been recorded sporadically from this location since (Trueman et al., 1992). A population was discovered on Wilsons Promontory (Davies, 1985), and its ecology has been studied in considerable detail (Sant and New, 1988; New, 1993). The recorded distribution of this species has greatly expanded with subsequent discoveries in Tasmania (Trueman et

Table 1. Collection sites, collection localities, habitats, habits and conservation threats of the nine species identified as of high conservation significance

Species	Sites	Distribution	Habitat	Habit	Conservation threats
Hemiphysalidae <i>Hemiphysalis mirabilis</i>	6	Vic., NE Tas.	swamps	clasper	cattle grazing, draining of swamps, burning of vegetation
Megapodagrionidae <i>Austroargiolestes isabellae</i>	8	SE NSW	bogs	unknown	urban and rural development
Gomphidae <i>Austrogomphus angeli</i>	4	SA, Vic.	unknown	unknown	unknown
Austropetaliidae <i>Archipetalia auriculata</i>	9	Tas.	montane	unknown	water pollution, burning of button grass
<i>Austropetalia patricia/A. tonyana</i>	7?	Vic., NSW	streams/bogs waterfalls	hider	forestry activities
Petaluridae <i>Petalura gigantea</i>	3	NSW, SE Qld	marshes	deep burrower	peat mining, rural development
Corduliidae <i>Archaeophya adamsi</i>	2	NSW	stream	hider	urban development
<i>S. gomphomacromioides</i>	22	Tas.	bogs	shallow burrower	water pollution, fire

al., 1992) and King Island (Endersby, 1993). During the preceeding two decades this species was believed to be extinct and subsequently placed on the endangered list in the IUCN Invertebrate Red Data Book. The recent papers of Trueman et al. (1992) and Watson (1995) suggested that since *H. mirabilis* is now known to have a more extensive distribution, it can no longer be regarded as endangered. Although this species has a wider distribution than previously thought, it is uncommon at the known sites (Hawking unpublished data) and is appraised as rare.

Megapodagrionidae *Austroargiolestes isabellae* Theischinger and O'Farrell

Austroargiolestes isabellae has only recently been recognised as a discrete species (Theischinger and O'Farrell, 1986). It appears to be restricted to the Sydney area and the Blue Mountains, where it is never common and should be considered rare. Watson et al., (1991) listed its habitat as streams and boggy seepages. The larva has not been recognised, and judging from the rarity of the adult, the larva will, most probably, also be rare, and its habitat will probably be unusual. This species is classified as rare, based on the restricted distribution and rarity of the adult, and that the identity and habitat of the larva is unknown.

Gomphidae *Austrogomphus angeli* Tillyard

Austrogomphus angeli is a little known species for which only about five adult specimens have been recorded. These were collected over a substantial length of the River Murray (900 km from Morgan, SA to Corowa, NSW) (Watson, 1991). They were recorded over a long time period: 58 years — Morgan (1909), Renmark (1948), Wentworth (1967) and Corowa (1967) (Watson, 1991). Watson (1991) recorded its adult habitat as mature, slow-flowing parts of the river, suggesting that the larva may in fact not be a stream-dweller. Hawking (1986) recorded the larva and its habitat as unknown.

This species must be given high conservation status, due to the limited numbers of adults having been collected and the larva not being collected. There is uncertainty with this species' existence and it is listed as indeterminate until a detailed survey can be undertaken. The distribution of this species corresponds to a section of River Murray that is under severe pressure from urban development (mainly building of holiday villages) and many agricultural activities (especially salination from irrigation practices).

Austropetaliidae *Archipetalia auriculata* Tillyard

Tillyard (1917) collected the first specimens of *Archipetalia auriculata* from Cradle Mountain, north-west Tasmania, at an elevation between 1100 and 1500 m, and considered it very rare. Allbrook (1979) listed *A. auriculata* from nine sites in the highlands of Tasmania, considering its distribution restricted and rare. The larvae are also rare. They occur in shallow streams, under exposed rocks and crevices in fallen timber (Allbrook 1979). This species is regarded as rare. Conservation appears plausible as these collection sites are all in either the Southwest National Park or Cradle Mountain Park. Hill and Michaelis (1988) listed the major threats as water pollution and fire.

Austropetaliidae *Austropetalia patricia* and *A. tonyana*

Tillyard (1909) described the adult and larvae of *Austropetalia patricia* from Leura, Blue Mountains and considered it an extremely rare species. Theischinger (1995) has re-examined the known specimens of *A. patricia* and from them described a new species, *A. tonyana*. Collectively these species occur along the Great Dividing Range in Victoria and New South Wales, with *A. tonyana* occurring from Canberra south, and *A. patricia* north from the Blue Mountains. The larvae occupy an unusual habitat, being found on logs or amongst moss in the splash zones of waterfalls. Many of the collection sites are protected as they occur in conservation areas, but sites outside these areas could be affected by forestry activities. These two archaic species are seldom collected, either as an adult or larva, and are considered uncommon. These species are listed as rare.

Petaluridae *Petalura gigantea* Leach

Petalura gigantea is Australia's largest dragonfly and its larvae live in burrows opening above water level (Tillyard, 1909). At present this species is only known from three locations: Katoomba (Blue Mountains National Park), Audley (Royal National Park) and Wingecarribee Swamp, Robertson. Specimens have been collected from near Tillyard's original site at Leura in the Blue Mountains and exuviae have been found in the Royal National Park, almost two years after the January 1994 bush fires destroyed 95% of the vegetation in the park (Theischinger, pers. comm.). The population at Wingecarribee Swamp may have become extinct, as neither adult nor larval stages have

been found recently. Wingecarribee Swamp is under threat from 'peat mining' operations which is destroying the larval habitat, through machinery removing the peat from the swamp and by the machinery clearing vegetation from the perimeter of the swamp. This species is listed as rare.

Corduliidae *Archaeophya adamsi* Fraser

Archaeophya adamsi is possibly the rarest dragonfly in south-eastern Australia. Only five adults of *A. adamsi* have been recorded; the holotype from Edungalba, Queensland, three specimens from Berowra Creek, near Hornsby and one male from Somersby Falls near Gosford, both sites in New South Wales (Theischinger and Watson, 1978). This species appears to have disappeared from the Edungalba and Berowra Creek sites and possibly only exists at Somersby Falls (Theischinger, pers. comm.). Fortunately the Somersby Falls site lies within the Brisbane Water National Park. Thus the natural habitat is being preserved, furthering the populations survival. However the site is under increasing pressure from agricultural activities, dairying and fruit growing, which are increasing in the upper catchment immediately upstream of the park. This species is listed as vulnerable.

Corduliidae *Austrocordulia leonardi*
Theischinger

Austrocordulia leonardi is a recent discovery. It was found in 1968 in low numbers from the Woronora River and Kangaroo Creek, south of Sydney (Theischinger, 1973). It seems to have disappeared from the Woronora River as the result of the Army demolishing a small weir on the river. Further investigations have revealed populations on the Nepean River at Maldon and at Audley in the Royal National Park (Theischinger, pers. comm. 1995). The discovery of the population in the Royal National Park will aid the conservation of this species which has a very restricted distribution and is listed as rare. In contrast, its congener *A. refracta* has a wide distribution and is extremely common.

Corduliidae *Synthemipsis*
gomphomacromioides Tillyard

Tillyard (1917) originally collected *Synthemipsis gomphomacromioides* from Cradle Mountain, north-west Tasmania, at an elevation of 1500 m. He gave details to distinguish the larva, but since then no larvae have been positively identified. Allbrook (1979) listed 19 collection

sites and suggested that this species was restricted to the swampy buttongrass plains at all altitudes, where it is locally common. Sant and Hayes (1990) agreed with Allbrook, reporting adults locally abundant in the Pelion area, Cradle Mountain and in the Mount Melaleuca area. Many of the collection sites of this species are in the Southwest National Park or Cradle Mountain Park. This species is listed as rare.

Discussion

The nine species investigated are all worthy of concern, having met the criteria to be given a conservation status ranking. Hill and Michaelis (1988) listed four species (*H. mirabilis*, *A. auriculata*, *S. gomphomacromioides* and *Austroaeschna hardyi*) from south-eastern Australia as of conservation concern and the first three species are listed as noteworthy species in this paper. However the last species, *A. hardyi*, has a wide distribution and is not given conservation status. A further seven species (*Austroargiolestes isabellae*, *Austrogomphus angeli*, *Austrocordulia leonardi*, *Austropetalia patricia*, *A. tonyana* and *Archaeophya adamsi*), not listed by Hill and Michaelis (1988), have been selected in this paper, for recommendation of conservation status. *Archaeophya adamsi* is classified as vulnerable, *Austrogomphus angeli* as indeterminate and the other seven species as rare (Table 2).

Much of the Australian odonate fauna is endemic and unique. All the species selected are endemic and have strong Gondwanan links. These relict dragonflies have very restricted distributions, their larvae are relict forms, and are found in unusual and different habitats (splash-zones of waterfalls, burrows etc.) (Table 1).

Archaeophya adamsi is probably the rarest dragonfly in south-eastern Australia and should receive prompt conservation attention to establish its distribution and habitat, and only then can preservation measures be implemented. *Austrogomphus angeli* has been listed as indeterminate, due to only a few specimens being collected, and these occurred over a wide range. The status can be established formally only after intensive collecting has been conducted and the species distribution, and larval identity and habitat are determined.

Habitat conservation is hampered in the cases of *Austroargiolestes isabellae* and *Austrogomphus angeli* because their larvae are not known and their ecology can not be characterised. Without this information recommendations to conserve their habitats cannot be suggested.

Table 2. The suggested conservation status of each species and conservation priorities for their habitats.

Species	Status	Conservation priorities
<i>Hemiphysalis mirabilis</i>	rare	preserve the known habitats
<i>Austroargiolestes isabellae</i>	rare	identify the larva and its habitat
<i>Austrogomphus angeli</i>	indeterminate	identify the larva and its habitat, determine its distribution
<i>Archipetalia auriculata</i>	rare	preserve the known habitats
<i>Austropetalia patricia</i>	rare	preserve the known habitats
<i>A. tonyana</i>	rare	preserve the known habitats
<i>Petalura gigantea</i>	rare	preserve the known habitats
<i>Archaeophya adamsi</i>	vulnerable	establish the distribution and habitat
<i>S. gomphomacromioides</i>	rare	identify the larva and its habitat

All the species suggested, except *A. angeli*, are found in montane areas, generally within National Parks or in State Parks (*H. mirabilis*), and with continued preservation and monitoring, these populations should remain viable. In contrast *A. angeli* occurs along the lower reaches of the River Murray, an area which has been heavily effected by salination from intensive irrigation and with very little chance of the degraded land being rehabilitated.

Much of the distributional data on Australian dragonflies on which this paper is based, has not been derived from commissioned surveys, but from naturalist collectors, post-graduate research students or scientists like Dr J.A.L. Watson. This type of collecting helps to build up databases of distributional information over a period of time, but cannot provide the detailed information of well designed commissioned surveys, such as the survey of the dragonflies of the Kakadu National Park conducted by CSIRO staff (Watson and Abbey, 1980). Detailed surveys should therefore be undertaken initially to establish the true status of these species. Once the status is known, conservation procedures can be implemented.

Currently there is no conservation strategy to preserve our unique Australia dragonflies. In the past the major conservation emphasis has been directed to the preservation of *H. mirabilis* (New 1993) and only recently Sydney Water has had Wingecarribee Swamp (a known habitat of *P. gigantea*) listed on the Australian Heritage Council's Register of the National Estate.

Conclusions and recommendations

The conservation of Australia Odonata has not developed at the same rate as urban expansion,

economic activity and the natural habitats of many dragonflies being destroyed. Preservation of habitats is urgent, but in the specific cases treated here, sites cannot be recommended until the distributions and ecology of the rare species are known. This can be achieved through initial surveys which should initiated immediately to determine the identity and ecology of the unknown larvae; and the distribution and population size of rare species.

From larval and ecological information, the following conservation recommendations can be suggested:

1. Conservation of natural aquatic and terrestrial habitat by including the sites in National Parks or as nature reserves, by purchasing the site if it is on private land;
2. Control pollution discharges to aquatic habitats through co-operation with the relevant private land owners and the states Environmental Protection Agency;
3. Transfer of conservation knowledge through education of non-specialists and children;
4. Monitor the success, or failures, of the above conservation measures and modify when necessary.

Conservation of Odonata depends on the protection of the adult and larval habitats which in many cases are very susceptible to destruction from urban and rural development.

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References

- Allbrook, P. 1997. *Tasmanian Odonata*. University of Tasmania: Hobart.
- Davies, D.A.L., 1985. *Hemiphlebia mirabilis* Selys: some notes on distribution and conservation status (Zygoptera: Hemiphlebiidae). *Odonatologica* 14: 331–339.
- Endersby, I.D., 1993. A new locality for *Hemiphlebia mirabilis* Selys (Odonata: Hemiphlebiidae). *Victorian Entomologist* 23: 4–5.
- Hawking, J.H., 1986. *Dragonfly larvae of the River Murray. A preliminary guide to the identification of known final instar odonate larvae of south-eastern Australia*. Albury-Wodonga Development Corporation, Wodonga [Technical Report No. 6].
- Hill, L. and Michaelis, F.B., 1987. *Conservation of insects and related wildlife*. Report on the Australian National Parks and Wildlife Service Survey of Insect Conservation Needs. Occasional Paper 13, Australian National Parks and Wildlife Service, Canberra. 40 pp.
- New, T.R., 1993. *Hemiphlebia mirabilis* Selys: recovery from habitat destruction at Wilsons Promontory, Victoria, Australia, and implications for conservation management (Zygoptera: Hemiphlebiidae). *Odonatologica* 22: 495–502.
- Sant, G.J. and Hayes, E.A., 1990. An investigation of four significant species of Odonata within the Southwest National Park of Tasmania. Report prepared for the Wilderness Ecosystem Baseline Study. 9 pp.
- Sant, G.J. and New, T.R., 1988. The biology and conservation of *Hemiphlebia mirabilis* Selys (Odonata: Hemiphlebiidae) in southern Victoria. *Arthur Rylah Institute for Environmental Research Technical Report* 82, v + 35 pp.
- Theischinger, G., 1973. Eine zweite Art der Gattung *Austrocordulia* Tillyard (Odonata: Anisoptera). *Annalen Naturhistorisches Museum, Wien* 77: 387–397.
- Theischinger, G., 1995. A second species of *Austropeitalia* Tillyard from Australia (Odonata: Austropeletiidae). *Linzer biol. Beitrage* 27: 291–295.
- Theischinger, G. and O'Farrell, A.F., 1986. The genus *Austroargiolestes* Kennedy (Zygoptera: Megapodagrionidae) *Odonatologica* 15: 387–428.
- Theischinger, G. and Watson, J.A.L., 1978. The Australian Gomphomacromiinae (Odonata: Corduliidae). *Australian Journal of Zoology* 26: 399–431.
- Theischinger, G. and Watson, J.A.L., 1984. Larvae of Australian Gomphomacromiinae, and their bearing on the status of the *Synthemis* group of genera (Odonata: Corduliidae). *Australian Journal of Zoology* 32: 67–95.
- Tillyard, R.J., 1909. Studies in the life-histories of Australian Odonata. No.1. The life-history of *Petalura gigantea* Leach. *Proceedings of the Linnean Society NSW* 34: 256–67.
- Tillyard, R.J., 1917. On some new dragonflies from Australia and Tasmania. (Order Odonata). *Proceedings of the Linnean Society NSW*. 42: 450–479.
- Trueman, J.W.H., Hoyer, G.A., Hawking, J.H., Watson, J.A.L. and New, T.R., 1992. *Hemiphlebia mirabilis* Selys: new localities in Australia and perspectives on conservation (Zygoptera: Hemiphlebiidae). *Odonatologica* 21: 367–374.
- Watson, J.A.L., 1991. The Australian Gomphidae (Odonata). *Invertebrate Taxonomy* 5: 289–441.
- Watson, J.A.L., 1995. The conservation status of the enigmatic Australian dragonfly *Hemiphlebia mirabilis* Selys. Pp. viii, 16–18 in: Corbet, P.S., Dunkle, S.W. and Ubukata, H. (eds), *Proceedings of the International Symposium on the conservation of dragonflies and their habitats*. Japanese Society for Preservation of Birds: Kushiro. xii + 70 pp.
- Watson, J.A.L. and Abbey, H.M., 1980. Dragonflies (Odonata) from the Northern Territory. *CSIRO Division of Entomology Report* 21: 1–44.
- Watson, J.A.L. and O'Farrell, A.F., 1991. Odonata (dragonflies and damselflies). In *The insects of Australia. 2nd edition*. Melbourne University Press: Melbourne.
- Watson, J.A.L., Theischinger, G. and Abbey, H.M., 1991. *The Australian Dragonflies. A guide to the identification, distributions and habitats of Australian Odonata*. CSIRO: Canberra and Melbourne.
- Wells, S.M., Pyle, R.M. and Collins, N.M., 1983. *The IUCN Invertebrate Red Data Book*. International Union for the Conservation of Nature: Gland, Switzerland. 434 pp.

A BIOCHEMICAL TAXONOMIC STUDY OF SPINY CRAYFISH OF THE GENERA *ASTACOPSIS* AND *EUASTACUS* (DECAPODA: PARASTACIDAE) IN SOUTH-EASTERN AUSTRALIA

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Abstract

Avery, L. and Austin, C.M., 1997. A biochemical taxonomic study of spiny crayfish of the genera *Astacopsis* and *Euastacus* (Decapoda : Parastacidae) in south-eastern Australia. *Memoirs of the Museum of Victoria* 56(2): 543-555.

A study of allozyme variation amongst spiny crayfish species of the genera *Astacopsis* (Huxley) and *Euastacus* Clark in south-eastern Australia was carried out to evaluate the current morphologically-based taxonomy. Nineteen populations representing ten putative species were analysed for variation at 32 allozyme loci. Heterozygosities were found to be low and typical for parastacid crayfishes. Significant geographical variation in allelic frequencies was found only in *E. yarraensis*. Analysis of genetic relationships amongst samples provided unambiguous support for the recognition for five *Euastacus* species (*E. armatus*, *E. kershawi*, *E. diversus*, *E. neodiversus* and *E. woiwuru*) and two species of *Astacopsis* (*A. gouldi* and *A. franklinii*). Support for the recognition of *A. tricornis* is equivocal as a sample of this species displayed a relatively low level of allozymic divergence from a sample of *A. franklinii*. Samples of *E. yarraensis* and *E. bispinosus* could not be distinguished from *E. armatus* indicating the need for more detailed taxonomic studies of this complex of species.

Introduction

Freshwater crayfish belonging to the genera *Astacopsis* (Huxley) and *Euastacus* Clark, commonly called spiny crayfish, are widespread in eastern Australia. *Euastacus* species occur only on mainland Australia in the states of Queensland, New South Wales, Victoria and South Australia, whereas *Astacopsis* species are found only in Tasmania (Clark, 1936; Riek, 1969). Both genera have a preference for cool, pristine and well-oxygenated freshwater environments and inhabit mostly permanent rivers, streams, lakes and impoundments. Spiny crayfish are found in both highland and lowland country in the cooler southern part of Australia but are restricted to more elevated and isolated areas in the northern part of their distribution (Swain et al., 1982; Morgan, 1983, 1986, 1988; Horwitz, 1990a; Hamr, 1992).

Several species of spiny crayfish are capable of growing to very large sizes. *Astacopsis gouldi* is the largest freshwater crayfish in the world and is known to reach sizes in excess of 3 kg (Olszewski, 1980) however, animals exceeding 2 kg are rarely caught today (Horwitz, 1990a). Several *Euastacus* species, including *E. armatus* (von Martens), *E. kershawi* (Smith) and *E. bispinosus* Clark from southern Australia are able to grow to weights in excess of 2 kg. As a consequence of

their large size all of these crayfish species have attracted considerable attention from amateur fishermen. The lower numbers of spiny crayfish being caught and their decreasing size over recent years have been attributed to the combination of increased recreational fishing pressure, habitat alteration and the slow growth of these species (Campbell, 1990; Honan and Mitchell, 1995). Conservation concerns have led to the implementation of a range of fishing regulations (Horwitz, 1990a; Anon, 1991; Linderhans and Rutzou, 1991) for *Euastacus* and *Astacopsis* species. In addition to fishing pressure, spiny crayfish also appear to be highly vulnerable to habitat change; significant range reductions have been recorded for several species and a number of species are now listed as rare or vulnerable (Horwitz, 1990a; Honan and Mitchell, 1995).

Studies of the biology and ecology of spiny crayfish species of both genera are scant (Clark, 1937; Hamr, 1992; Honan and Mitchell, 1995). However, in contrast, the taxonomy of these crayfish has been comprehensively examined by several authors in recent years (Riek, 1969; Swain et al., 1982; Morgan, 1983, 1986, 1988; Hamr, 1992) using classical morphologically-based approaches. These studies have led to major taxonomic rearrangements and, at times, contradictions indicating that morphological

variation is extensive and complex within these crayfish. Thus, despite these recent taxonomic studies there are still doubts concerning the number and identity of species within both *Astacopsis* and *Euastacus* (see taxonomic history).

According to the biological species concept, species consist of groups of individuals potentially capable of exchanging genetic material with each other and producing viable offspring, but are reproductively isolated from other such groups (Mayr, 1963). While this definition has conceptual merits it is difficult to put into practice as studies aimed at the direct identification of reproductive groups are demanding and rarely undertaken by taxonomists. Further, even when reproductive studies are conducted the interpretation of results is often equivocal. An advantage of using biochemical and molecular genetic techniques to address taxonomic questions is that they can be used to indirectly establish or infer reproductive relationships amongst populations (Richardson et al., 1986) thus providing information consistent with the biological definition of species. In addition, a number of studies have shown biochemical data to be very useful in resolving species boundaries where morphological variation is difficult to interpret (Richardson et al., 1986).

Australian freshwater crayfish are a taxonomically difficult group and the technique of allozyme electrophoresis has proven useful in the delineation of species boundaries in the genera *Cherax* (Austin, 1986, 1996; Campbell et al., 1994; Austin and Knott, 1996) *Engaeus* (Horwitz et al., 1990) and *Gramastacus* (Zeidler and Adams, 1990). The aim of this project was to extend these biochemical taxonomic studies of Australian parastacid crayfish to spiny crayfish by evaluating the morphologically-based taxonomy of the genus *Astacopsis* and Victorian species of the genus *Euastacus* using allozyme gel electrophoresis.

Taxonomic history

The first taxonomic record of an Australian freshwater crayfish was a spiny crayfish described by Shaw in 1794 as *Cancer serratus*. This species was subsequently placed in the genus *Astacopsis*, erected by Huxley (1878), who placed the genus within the newly described family, the Parastacidae, which accommodated all the crayfish from the southern hemisphere. Since this early work there have been two major revisions of the family Parastacidae, by Clark (1936) and Riek (1969). Clark (1936) divided

the spiny crayfish into two genera, *Astacopsis* and *Euastacus*. She restricted *Astacopsis* to the Tasmanian spiny crayfish to which she added two new species, giving a total of three species for this genus. At the same time she erected a new genus, *Euastacus*, for the Australian mainland spiny crayfish which at that time contained 11 species. In a subsequent revision of *Euastacus* Clark (1941) retained only four of these previously described species, elevated two from subspecies and described three new species thereby recognising nine species in the genus.

The next major contributor to the taxonomy of spiny crayfish was Riek (1956, 1969). Riek (1956) split *Euastacus* by erecting the genus *Euastacoides* for several small species which have restricted distributions in northern New South Wales and southern Queensland. In his major revision of Australian parastacid crayfish (Riek, 1969) he retained the three spiny crayfish genera and described an additional species for *Astacopsis*, bringing the number of species within this genus up to four. He also described a number of new species of mainland spiny crayfish bringing the total number of *Euastacus* species up to 27.

A relatively recent revision of *Astacopsis* by Swain et al. (1982) reduced the species number from four to two, however Hamr (1992) re-established the three species originally described by Clark (1936). The most recent revisions of *Euastacus* have been by Morgan (1983, 1986, 1988, 1989) who undertook a comprehensive and detailed review of *Euastacus* throughout its distribution which resulted in the synonymy of *Euastacoides* with *Euastacus* and the recognition of a total of 37 species within the redefined genus which included 16 newly described species (Morgan, 1983, 1986, 1988, 1989; Horwitz, 1995).

Materials and methods

Sample collection

The majority of *Euastacus* and *Astacopsis* specimens were collected during the day from rivers and streams in state parks and on private land. Collection techniques consisted of the use of baited strings, drop nets in rivers and deep streams and the turning over of rocks in shallow streams. The specimens of *E. neodiversus* from Tarwin River West were dug from burrows in the river bank. Wherever possible each species examined in this study was sampled from the

Table 1. OTU code, sample size (n) and collecting locality for each population of *Euastacus* species and *Astacopsis* species sampled in Victoria and Tasmania.

Species	OTU	n	Locality
Victoria			
<i>E. kershawi</i>	EK-a	1	Shady Creek, NE of Warragul, Vic.
<i>E. kershawi</i>	EK-b	1	Tarra River, Yarram, Vic.
<i>E. bispinosus</i>	EB-a	2	Crawford River, Dirk Dirk, Vic.
<i>E. neodiversus</i>	EN-a	2	Dingo Creek, N of Welshpool, Vic.
<i>E. neodiversus</i>	EN-b	2	Turtons Creek, S of Mirboo, Vic.
<i>E. neodiversus</i>	EN-c	4	Tarwin River West, Vic.
<i>E. woiwuru</i>	EW-a	2	Olinda Creek, Olinda, Vic.
<i>E. woiwuru</i>	EW-b	1	Sassafras Ck., Monbulk, Vic.
<i>E. woiwuru</i>	EW-c	3	Dandenong National Park, Vic.
<i>E. yarraensis</i>	EY-a	4	Stephensons Falls, Gellibrand River, Vic.
<i>E. yarraensis</i>	EY-b	2	Aire River, S. of Beach Forest, Vic.
<i>E. yarraensis</i>	EY-c	2	Lake Elizabeth, E Barwon River, Vic.
<i>E. yarraensis</i>	EY-d	1	Williamsons Ck, Ballarat, Vic.
<i>E. yarraensis</i>	EY-e	3	Woori Yallock Creek, Vic.
<i>E. diversus</i>	ED-a	1	Orbost, Vic.
<i>E. armatus</i>	EA-a	1	Ovens River. Harrietville, Vic.
Tasmania			
<i>A. tricornis</i>	AT-a	3	Arve River, Mt. Hartz road. Tas.
<i>A. franklinii</i>	AF-a	3	New Town rivulet, Nth. Hobart, Tas.
<i>A. gouldi</i>	AG-a	1	Big River, Wynard, Tas.

type locality or from other sites referred to in the literature (Clark, 1936; Morgan, 1986; Hamr, 1992). The species sampled, population codes and locality descriptions are given in Table 1. Specimens were either frozen in the field in liquid nitrogen or kept alive on ice until transferred to the laboratory.

Tissue samples

Each crayfish specimen was initially stored in a labelled polythene freezer bag at -20°C . Frozen specimens were placed in liquid nitrogen and sent to the Evolutionary Biology Unit of South Australian Museum, where they were stored at -80°C . Abdominal muscle tissue was dissected from thawed specimens and placed in a plastic vial with an equal volume of lysing solution (500 ml of distilled water containing 50 mg NADP and 0.5 ml β -mercaptoethanol). This mixture was homogenised using a Branson Sonifier (model B-12) and then centrifuged for 10 min. The supernatant was removed and stored in Micro-Haematocrit Capillary Tubes which were then held at -80°C until required. All carcasses were preserved in 7% formalin.

Electrophoresis

A pilot study carried out with *Euastacus* species using starch gel electrophoresis identified twenty enzymatic loci but using cellulose acetate gels ('Cellogel') forty three enzymatic loci could be, therefore only 'Cellogel' was used in all subsequent electrophoresis runs. However, 11 loci proved to be too difficult to score consistently across all species and so were excluded from the final analysis. The remaining 32 loci were screened for all samples and are presented in Table 2 with their abbreviations, enzyme commission (EC) numbers and details of running conditions. The general procedures for running 'Cellogel' electrophoresis are given by Richardson et al. (1986).

Zymograms were interpreted using standard approaches (Richardson et al., 1986). Putative allozymes were designated by letters in the order of mobility starting with the slowest migrating allozyme and were scored as genotypes. Allelic frequencies, heterozygosities and Nei's genetic identity (I) corrected for small sample size (Nei, 1978) were calculated using BIOSYS-1 (Swof-

Table 2. Stains and buffers used in the electrophoretic analysis of *Astacopsis* and *Euastacus* samples.

Enzyme name	Abbreviation	E.C.number ¹	No. of loci	buffer ²
Aconitase hydratase	Acon	4.2.1.3	2	B
Aminoacylase	Acyc	3.5.1.14	1	C
Fructose-bisphosphate aldolase	Ald	4.1.2.13	1	B
Arginine kinase	Argk	2.7.3.3	1	C
Enolase	Enol	4.2.1.11	1	B
Fructose-1, 6-diphosphatase	Fdp	3.1.3.11.	1	B
Alanine aminotransterase	Gpt	2.6.1.9	1	B
Guanine deaminase	Gda	3.5.4.3	1	C*
Lactoyl-glutathione lyase	Glo	4.4.1.5	1	C
Aspartate aminotransferase	Got	2.6.1.1	2	B
General protein	Gp	—	1	C
Glucose-6-phosphate isomerase	Gpi	5.3.1.9	1	B
Isocitrate dehydrogenase	Idh	1.1.1.42	2	B
Lactate dehydrogenase	Ldh	1.1.1.27	1	B
Malate dehydrogenase	Mdh	1.1.1.37	2	B/C
'Malic' enzyme	Me	1.1.1.40	1	B
Mannose-6-phosphate isomase	Mpi	5.3.1.8	1	B
Nucleoside-diphosphate kinase	Ndpk	2.7.4.6	1	B
Dipeptidase	Pep A	3.4.13.X	1	C
Tripeptidase aminopeptidase	Pep-B	3.4.11.X	1	A
Dipeptidase	Pep-C	3.4.13.X	1	C
Phosphoglycerate mutase	Pgam	2.7.5.3	1	B/C
Phosphogulyolate dehydrogenase	6PgD	1.1.1.44	1	B*
Phosphoglycerate kinase	Pgk	2.7.2.3	1	C
Phosphoglucomutase	Pgm	2.7.5.1	2	C
Pyruvate kinase	Pk	2.7.1.40	1	B
Triose-phosphate isomerase	Tpi	5.3.1.1	1	B/C

¹enzyme commission number²buffers used: A=0.01M citrate-phosphate, pH 6.4

B=0.02M phosphate, pH7.0

B*=20 mg NADP and 8.5 mg MgCl₂ in 300 ml soaking solution

C=0.05M Tris-maleate, pH 7-8

C*=0.05M Tris-maleate, pH 7-8 with 1mM MgCl₂

ford and Selander, 1981) from genotypic data. A matrix of percentage fixed allelic differences was calculated for each pairwise combination of OTUs (Richardson et. al., 1986). Nei's genetic identity (I) and percentage fixed allelic differences were calculated using only the loci which stained in both OTUs. Dendrograms were constructed using the unweighted pair group method with arithmetic averages (UPGMA) technique (Sneath and Sokal, 1973) from the matrices of percentage fixed differences and

Nei's genetic identity using Phylip, version 3.56 (Felsenstein, 1982).

Although it may appear that the sample sizes used in this study with respect to the number of individual crayfish per population are small, it has been established that for taxonomic applications the number of individuals from specific locations does not need to be large as long as these individuals are scored for a relatively large number of electrophoretic loci (Richardson et. al., 1986; Nei, 1978).

Results

Allelic variation amongst OTUs was recorded at 30 loci; two loci, Gpt and Ldh, were invariant (Table 3). The average estimated heterozygosities per locus (H_E), observed heterozygosities (H_O) and proportion of polymorphic loci (P) for each OTU are given in Table 4. Observed heterozygosities (H_O) for both genera are low, ranging from 0.0 to 0.078. The weighted average heterozygosities (H_O) for *Euastacus* and *Astacopsis* are 0.028 and 0.024 respectively. For each sample set H_O and H_E do not differ substantially from each other as indicated by the overlapping standard errors.

Genetic relationships amongst all populations of *Euastacus* and *Astacopsis* are summarised in Table 5 with Nei's genetic identities given in the lower diagonal and percentage fixed differences given in the upper diagonal. Figure 1 shows a dendrogram of the relationships amongst samples derived from percentage fixed differences. As the UPGMA dendrogram based upon Nei's genetic identities was very similar to Figure 1 it is not shown.

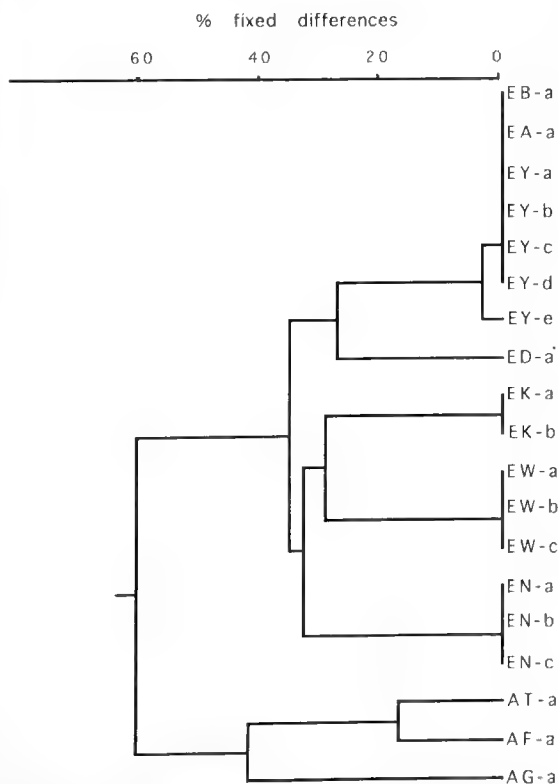


Figure 1. UPGMA dendrogram derived from a matrix of % fixed differences (see Table 1 for sample codes).

From these analyses (Table 5 and Figure 1) it can be seen that there is a primary split between the Victorian *Euastacus* species and the Tasmanian *Astacopsis* species which share an average genetic identity of $I = 0.34$. Amongst the three *Astacopsis* species, *A. gouldi* (AG-a) is quite distinct sharing an average genetic similarity of $I = 0.51$ and $I = 0.52$ with *A. tricornis* (AT-a) and *A. franklinii* (AF-a) respectively. Although distinct from each other, *A. tricornis* (AT-a) and *A. franklinii* (AF-a) share a much higher similarity ($I = 0.82$) than either does with *A. gouldi* (AG-a).

From Figure 1 it can be seen that although seven putative species of *Euastacus* were examined only five distinct clusters are apparent. Four of these clusters correspond to the species *E. kershawi* (EK-a and -b), *E. diversus* (ED-a), *E. neodiversus* (EN-a, -b and -c) and *E. woiwuru* (EW-a, -b and -c) as delineated by Morgan (1986). The distinctiveness of these taxa is clearly reflected by their genetic identity values (Table 5). The genetic identity values within species are small ($I = 0.97$ – 1.00) compared with the differences amongst species ($I = 0.49$ – 0.68). In terms of fixed allelic differences, comparisons between populations within species showed no fixed differences, whereas between-species differences ranged from eight to nine fixed differences.

In contrast to these clear cut differences, the fifth cluster groups the populations of three species together, viz. *E. yarraensis* (EY-a, -b, -c, -d and -e), *E. bispinosus* (EB-a) and *E. armatus* (EA-a) which share a high degree of genetic similarity ($I = 0.89$ – 1.00). No fixed allelic differences were found amongst these three putative species. The only sample within this cluster which is even slightly divergent is the most easterly sample of *E. yarraensis* which differs by one fixed differences from the more westerly samples of this species. Thus, the western samples of *E. yarraensis*, EY-a, -b, -c and -d, are in fact more closely related to *E. armatus* and *E. bispinosus* ($I = 0.98$ – 1.00) than to the eastern sample of this species, EY-e ($I = 0.91$ – 0.92).

Discussion

Heterozygosities

The average observed heterozygosities (H_O) found in *Euastacus* and *Astacopsis* agree with the low values recorded in decapods (Tracey et al., 1975; Mulley and Latter, 1980; Nelson and Hedgecock, 1980; Hedgecock et al., 1982) and with those found previously for spiny crayfish (*E.*

Table 3. Allele frequencies at each locus. Where allele frequencies are not given the frequency is 1.00. Alleles are listed alphabetically in order of increasing distance from the cathode. Sample sizes are given below OTU codes. Asterisks indicates the failure of enzyme to stain at that particular locus.

Locus	EB-a	EA-a	EY-a	EY-b	EY-c	EY-d	EY-e	ED-a	EK-a	EK-b	EW-a	EW-b	EW-c	EN-a	EN-b	EN-c	AT-a	AF-a	AG-a
	2	1	4	2	2	1	3	1	1	1	2	1	3	2	2	4	3	3	1
Acon-1	a	***	a	a	a	a	a	a	a	a	a(0.25) b(0.75)	b	b	a	a	a	c	c	c
Acon-2	a	***	a	a	a	a	a	***	a	a	a	a	a	a	a	a	a	b	***
Acyc	b	b	b	b	b	b	b	b	a(0.50) b(0.50)	a(0.50) b(0.50)	a	a	***	b	b	b	***	***	***
Ald	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a	a	b(0.83) c(0.17)	b	b
Argk	b	b	b	b	b	b	b	b	b	b	b	b	b	c	c	c	a	a	b
Enol	b	b	b	b	b	b	b	b	b	b	b(0.83) d(0.17)	b	b(0.75) d(0.25)	b	b	b	a	a	c
Fdp	c	c	c	c	c	c	c	c	a	a	a(0.75) b(0.25)	a(0.50) b(0.50)	a	c	c	c	d	d	c
Gpt	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Gda	b	b	b	b	b	b	b	***	d	d	d	d	d	d	d	d	a	c	***
Glo	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a
Got-1	b	b	b	b	b	b	b	b	b	b	c	b(0.50) c(0.50)	c	b	b	b	a	a	***
Got-2	d	d	d	d	d	d	b(0.67) d(0.33)	b(0.50) d(0.50)	b	b	c	c	c	b	b	b	a	a	b
Gp	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a
Gpi	b	b	b	b	b	b	b	b	b	b	b(0.75) c(0.25)	b	b(0.83) c(0.17)	a(0.50) b(0.50)	a(0.50) b(0.50)	b	c	b(0.33) c(0.67)	c
Idh-1	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b
Idh-2	b	b	b	b	b	b	b(0.50) c(0.50)	b	a	a	b	b	b	a	a	a	c	c	***
Ldh	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Mdh-1	b	b	b	b	b	b	a(0.67) b(0.33)	b	b	b	b	b	b	b	b	b	b	b	b
Mdh-2	b	b	b	b(0.75) c(0.25)	b	b	b(0.33) c(0.67)	a	b	b	b	b	a(0.50) b(0.50)	b	b	b	b	b	b

Table 3. Continued

Locus	EB-a	EA-a	EY-a	EY-b	EY-c	EY-d	EY-e	ED-a	EK-a	EK-b	EW-a	EW-b	EW-c	EN-a	EN-b	EN-c	AT-a	AF-a	AG-a
Me	2 c	1 c	4 c	2 b(0.50) c(0.50)	2 c	1 c	3 c	1 c	1 c	1 c	2 a	1 a	3 a	2 a	2 a(0.75) b(0.25)	4 a	3 a	3 a	1 a
Mpi	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a
Ndpk	b	b	b	b	b	a	b	a	b	b	b	b	b	b	a(0.50) b(0.50)	a(0.13) b(0.87)	b	b	b
Pep-A	d	***	d	d	d	d	d	c	c	c	d	d	d	d	d	d	a	b	b
Pep-B	d	d	d	d	d	c(0.50) d(0.50)	d	c	a	a	b	b	b	c	c	c	f	d	e
Pep-C	a	***	a	a	a	a	a	d	c	c	b	b	b	b	b	b	***	***	***
Pgam	b	b	b	b	b	b	b	b	a	a	a(0.25) b(0.75)	a	a(0.83) b(0.17)	b	b	b	b	a(0.50) b(0.50)	b(0.50) c(0.50)
6Pgd	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a(0.87) b(0.13)	b	b	a
Pgk	c	c	c	c	c	a	c	a	a	a	a	a	a	c	c	c	b	b	b
Pgm-1	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	c
Pgm-2	d	d	d	d	d	d	d	b	c	c	b	b	b	b	b	b	a	b	a
Pk	c	c	c	c	c	c	b	c	b	b	b	b	b	b	b	b	a	a	b
Tpi	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	b	b	b

Table 4. Sample size (n), percentage of polymorphic loci (P)¹, average estimated heterozygosities per locus (H_E) and the observed heterozygosities per locus (H_O), (standard errors in parentheses) for each OTU.

Population	n	P(%)	H _O (SE)	H _E (SE)
<i>E. bispinosus</i> -a	2	0.0	0.000	0.000
<i>E. armatus</i> -a	1	0.0	0.000	0.000
<i>E. yarraenesis</i> -a	4	0.0	0.000	0.000
<i>E. yarraenesis</i> -b	2	0.0	0.000	0.000
<i>E. yarraenesis</i> -c	2	6.3	0.047 (0.034)	0.036 (0.026)
<i>E. yarraenesis</i> -d	1	6.3	0.063 (0.043)	0.063 (0.043)
<i>E. yarraenesis</i> -e	3	9.4	0.000	0.050 (0.028)
<i>E. diversus</i> -a	1	3.1	0.031 (0.031)	0.031 (0.031)
<i>E. kershawi</i> -a	1	3.1	0.031 (0.031)	0.031 (0.031)
<i>E. kershawi</i> -b	1	3.1	0.031 (0.031)	0.031 (0.031)
<i>E. woiwuru</i> -a	2	15.6	0.078 (0.033)	0.078 (0.033)
<i>E. woiwuru</i> -b	1	6.3	0.063 (0.043)	0.063 (0.043)
<i>E. woiwuru</i> -c	3	12.5	0.042 (0.020)	0.050 (0.025)
<i>E. neodiversus</i> -a	2	3.1	0.031(0.031)	0.021 (0.021)
<i>E. neodiversus</i> -b	2	9.4	0.078 (0.046)	0.057 (0.032)
<i>E. neodiversus</i> -c	4	6.3	0.016 (0.011)	0.016 (0.011)
<i>A. tricornis</i> -a	3	3.1	0.010 (0.010)	0.010 (0.010)
<i>A. franklinii</i> -a	3	6.3	0.031 (0.023)	0.035 (0.025)
<i>A. gouldi</i> -a	1	3.1	0.031 (0.031)	0.031 (0.031)

¹ A locus is considered polymorphic if the frequency of the most common allele does not exceed 95%.

bispinosus and *E. armatus*) by Campbell (1990) and for land crayfish (*Engaeus* spp.) by Horwitz et al. (1990). A possible explanation for low heterozygosity levels is that the effective population sizes of spiny crayfish may fall below the number of reproducing adults required to prevent the loss of genetic diversity through inbreeding effects. This can be caused by 'bottlenecks', which are drastic reductions in population size. The effects of a severe bottleneck on heterozygosity may be extremely long lived, in the order of 10⁶ generations (Hedgewick et al., 1982). The duration of bottleneck effects are extended further in species with low rates of population increase. Recent ecological studies have found that spiny crayfish are slow to reach maturity, are long lived and frequently have small population sizes (Lindermans and Rutzou, 1991; Honan and Mitchell, 1995) which means that populations of these crayfish would be both prone to bottleneck events and slow in recovering from them.

Delineation of species

Generally accepted principles for the interpretation of electrophoretic data in relation

to taxonomic studies have been established (Thorpe, 1982; Richardson et al., 1986) and have been applied to parastacid crayfish species by Horwitz et al. (1990), Zeidler and Adams (1990), Campbell et al. (1994), Austin (1986, 1996) and Austin and Knott (1996). These principles set guidelines for delineating species by using fixed allelic differences or levels of genetic similarity. For example, if allopatric populations have less than 15% fixed differences or genetic identities of 0.85 or greater they are generally considered to be conspecific, conversely if populations have greater than 15% fixed differences or genetic identities less than 0.85 they are usually considered to be separate species. As the results of applying the recommendations of Richardson et al. (1986) using percent fixed difference and those of Thorpe (1982) based on genetic similarity are very similar, only the former will be discussed here on.

Using the criteria of Richardson et al. (1986) the recognition of five species of *Euastacus* (*E. armatus*, *E. kershawi*, *E. diversus*, *E. neodiversus* and *E. woiwuru*) and three species of *Astacopsis* (*A. gouldi*, *A. franklinii* and *A. tricornis*) is supported by the allozyme data (Table 6). The find-

Table 5. Summary of genetic relationships amongst 19 populations of spiny crayfish derived from 32 loci. Above the diagonal are given percentage fixed differences and below the diagonal are given Nei's unbiased identity (I).

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
<i>E. bispinosus-a</i> (1)	*	0.0	0.0	0.0	0.0	0.0	0.0	3.1	26.6	34.3	34.3	31.2	27.5	38.7	34.4	34.3	34.3	70.0	63.3	50.0
<i>E. armaus-a</i> (2)	1.000	*	0.0	0.0	0.0	0.0	0.0	3.5	22.2	32.1	32.1	39.2	39.2	38.7	35.7	35.7	39.2	69.2	62.5	50.0
<i>E. yarraensis-a</i> (3)	1.000	1.000	*	0.0	0.0	0.0	0.0	3.1	26.6	34.3	34.3	37.5	43.7	37.0	34.3	34.3	34.3	66.6	65.5	53.8
<i>E. yarraensis-b</i> (4)	0.994	1.000	0.994	*	0.0	0.0	0.0	3.1	26.6	34.3	34.3	37.5	40.6	38.7	34.3	31.2	34.3	66.6	65.5	53.0
<i>E. yarraensis-c</i> (5)	1.000	0.994	1.000	0.994	*	0.0	0.0	3.1	26.6	34.3	34.3	37.5	40.6	38.7	34.3	34.3	34.3	66.6	65.5	53.8
<i>E. yarraensis-d</i> (6)	0.989	0.982	0.984	0.977	0.984	*	0.0	3.1	26.6	28.1	28.1	37.5	40.6	38.7	34.3	34.3	34.3	63.3	62.5	53.8
<i>E. yarraensis-e</i> (7)	0.908	0.920	0.909	0.910	0.909	0.891	*	34.3	28.1	28.1	34.3	37.5	35.4	34.3	34.3	34.3	34.3	66.6	71.8	53.8
<i>E. diversus-a</i> (8)	0.723	0.766	0.723	0.723	0.720	0.752	0.635	*	30.0	30.0	40.0	46.6	41.3	31.2	30.0	30.0	30.0	72.4	71.8	57.6
<i>E. kershawi-a</i> (9)	0.649	0.667	0.646	0.634	0.646	0.656	0.663	0.678	*	0	28.1	28.1	32.2	37.5	37.5	37.5	37.5	70.0	68.7	53.8
<i>E. kershawi-b</i> (10)	0.655	0.667	0.651	0.604	0.651	0.662	0.669	0.678	1.000	*	28.1	28.1	32.2	37.5	37.5	37.5	37.5	70.0	68.7	53.8
<i>E. woiwuru-a</i> (11)	0.599	0.602	0.596	0.601	0.596	0.589	0.591	0.509	0.656	0.651	*	0.0	0.0	0.0	28.1	28.1	28.1	60.0	65.6	50.0
<i>E. woiwuru-b</i> (12)	0.590	0.600	0.587	0.591	0.587	0.581	0.578	0.496	0.688	0.683	0.980	*	0.0	0.0	31.2	31.2	31.2	66.6	65.6	57.6
<i>E. woiwuru-c</i> (13)	0.574	0.586	0.574	0.574	0.581	0.567	0.590	0.513	0.662	0.699	0.990	0.976	*	29.0	29.0	29.0	29.0	60.0	59.3	50.0
<i>E. neodiversus-a</i> (14)	0.656	0.633	0.647	0.652	0.647	0.674	0.665	0.646	0.636	0.642	0.687	0.674	0.667	*	0.0	0.0	0.0	66.6	68.7	50.0
<i>E. neodiversus-b</i> (15)	0.652	0.628	0.644	0.652	0.644	0.670	0.661	0.676	0.633	0.638	0.676	0.662	0.655	1.000	*	0.0	0.0	66.6	68.7	50.0
<i>E. neodiversus-c</i> (16)	0.662	0.640	0.654	0.658	0.654	0.680	0.671	0.661	0.643	0.648	0.691	0.680	0.671	0.998	0.993	*	63.3	68.7	50.0	
<i>A. tricornis-a</i> (17)	0.330	0.329	0.330	0.330	0.328	0.352	0.293	0.248	0.296	0.296	0.350	0.307	0.304	0.305	0.285	0.304	*	16.6	42.3	*
<i>A. franklini-a</i> (18)	0.334	0.372	0.334	0.334	0.332	0.340	0.297	0.279	0.300	0.300	0.352	0.340	0.328	0.298	0.278	0.303	0.820	*	42.3	*
<i>A. gouldi-a</i> (19)	0.408	0.484	0.408	0.408	0.407	0.412	0.434	0.353	0.427	0.427	0.434	0.392	0.391	0.412	0.393	0.402	0.521	0.519	*	*

ing of fixed allelic differences ranging from 22.2 to 46.6% for *Euastacus* and 16.6 to 42.3% for *Astacopsis* is similar to the findings for others parastacid crayfish by Austin (1986, 1996) and Austin and Knott (1996) for species of *Cherax* and by Horwitz et al. (1990) for species of *Engaeus*.

Of the eight species of spiny crayfish recognised above, the separation of *A. franklinii* from *A. tricornis* is the most doubtful on the basis of both allozyme and morphological evidence. These two species represent the most closely related pair of taxa recognised in this study with only 16.6% fixed differences, which is only marginally above the recommended 15% level (Richardson et al., 1986) for delineating species. Zeidler and Adams (1990) synonymised the crayfish species *Gramastacus insolitus* and *G. gracilis*, which were found to have a fixed allelic difference of 14%. Thus, the allozyme evidence supporting the recognition of *A. tricornis* is not strong based on a rigid interpretation of the genetic-yardstick approach. However, the allozyme differences between the sample of this species and the sample of *A. franklinii* are reasonably substantial given their close geographic proximity (less than 100 km) and given that geographic variation in allozyme frequencies tends to be low in spiny crayfish species (Campbell, 1990, this study).

The morphological evidence supporting the status of *A. tricornis* is also far from unequivocal. Swain et al. (1982) did not consider there were sufficient morphological differences to warrant the separation of *A. tricornis* from *A. franklinii* on the basis of an examination of variation in a

range of morphological characteristics. In particular they noted that 'spininess' which can include the 'tricorn' rostral tip of *A. tricornis*, increases with crayfish size. In contrast, Hamr (1992) re-established *A. tricornis* on the basis of variation in a limited number of characters associated with the rostrum, size and general spininess. Clearly, the taxonomy of these two species of *Astacopsis* needs to be clarified and would benefit from a more detailed study of both morphological and allozyme variation.

Morgan (1986) expressed some concern about the specific status of *E. woiwuru* in relation to *E. neodiversus* because he could only distinguish between them on the basis of minor differences in spination. He described them as a 'species complex', which according to Mayr's (1963) definition would warrant their recognition as subspecies. However, the results of this study clearly indicate that recognition of these two species is justified as they show a high level of electrophoretic divergence from each other.

The status of *E. diversus* is somewhat uncertain as only a very limited number of specimens have been located from a restricted geographical range in north eastern Victoria (Morgan, 1986). This study clearly distinguishes *E. diversus* from the other taxa examined in this study and worthy of the endangered species status it has been given by the Victorian Department of Conservation and Natural Resources. It will, however, be necessary to compare samples of *E. diversus* with the morphologically similar *E. bidawalus* (Morgan, 1986) to verify it is in fact a genetically distinct species. If there are no major genetic differences between these two species then both the

Table 6. Comparison between the current classification of spiny crayfish in south eastern Australia and a classification supported by this study.

Current taxonomy	This study
<i>E. diversus</i>	<i>E. diversus</i>
<i>E. kershawi</i>	<i>E. kershawi</i>
<i>E. woiwuru</i>	<i>E. woiwuru</i>
<i>E. neodiversus</i>	<i>E. neodiversus</i>
<i>E. armatus</i>	<i>E. armatus</i>
<i>E. yarraensis</i>	<i>E. armatus</i>
<i>E. bispinosus</i>	<i>E. armatus</i>
<i>A. gouldi</i>	<i>A. gouldi</i>
<i>A. franklinii</i>	<i>A. franklinii</i>
<i>A. tricornis</i>	<i>A. tricornis</i> (<i>A. franklinii</i> ?)

current taxonomy and the conservation status of *E. diversus* will need to be reviewed.

The most surprising finding of this study was the failure to separate *E. bispinosus* and *E. yarraensis* from *E. armatus*. Strict application of the criteria for interpreting allozyme data suggest that only one widespread and morphologically variable species, *E. armatus*, should be recognised. Morgan (1986) observed that *E. armatus* and *E. yarraensis* are morphologically similar species and, although he notes similarities between *E. bispinosus* and *E. kershawi*, he couples *E. bispinosus* with *E. armatus* and *E. yarraensis* in his taxonomic key. In fact the major differences amongst *E. armatus*, *E. yarraensis* and *E. bispinosus* recorded by Morgan (1986) essentially relate to the degree of spination of the thorax and abdomen. Given the concerns expressed by Swain et al. (1982) and Austin and Knott (1996) on the taxonomic reliability of characters relating to 'spininess' in relation to *Astacopsis* spp. and to *Cherax* spp. respectively, the morphological evidence supporting the distinctiveness of these *Euastacus* species is not strong. A more detailed assessment of morphological variation within this complex of species is clearly warranted. This group of species would benefit from an examination of DNA variation using a more sensitive molecular genetic technique than allozyme electrophoresis for resolving fine-scale genetic differences amongst populations.

Phylogenetics

Although this study is being extended to an examination of phylogenetic relationships amongst spiny crayfish using numerical cladistic techniques (Austin and Avery, in prep.) it is worth commenting on the relationship between *Euastacus* and *Astacopsis*. Morgan (1983) considered the phylogeny of spiny crayfish using as a 'primary' character the male cuticle partition, which is found in *Astacopsis* and several species of *Euastacus* from south-eastern Victoria (*E. bidawalus*, *E. diversus*, *E. neodiversus* and *E. woiwuru*). He considered species possessing a partition to be more closely related to each other than those lacking a partition, which supports the widening of the taxonomic definition of *Astacopsis* to encompass mainland species. Consistent with this possibility, several species of freshwater crayfish are known to occur both in northern Tasmania and the extreme south of mainland Australia (Riek, 1969; Horwitz 1988, 1990b) indicating that Bass Strait has not been a significant barrier to the dispersal of freshwater

crayfish. Further, the findings by Patak and Baldwin (1984) of very few immunochemical differences in the haemocyanins between the two spiny crayfish genera is also consistent with Morgan's theory of a possible close relationship. The finding in this study of significant allozyme differences between the *Astacopsis* and *Euastacus* species and their clustering into two discrete groups (Figure 1), however, supports the present taxonomic delineation of these genera in south-eastern Australia.

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References

- Anon, 1991. *Freshwater fish of Victoria. Spiny freshwater crayfish*. Department of Conservation and Environment-Fisheries Management Division. Inland Fisheries Management Branch. Victoria.
- Austin, C.M., 1986. *Electrophoretic and morphological systematic studies of the genus Cherax (Decapoda: Parastacidae) in Australia*. Unpublished Ph. D. Thesis, University of Western Australia.
- Austin, C.M., 1996. An electrophoretic and morphological taxonomic study of the freshwater crayfish genus *Cherax* Erichson (Decapoda: Parastacidae) in northern and eastern Australia. *Australian Journal of Zoology* in press.
- Austin, C.M. and Knott, B., 1996. Systematics of the freshwater crayfish genus *Cherax* Erichson (Decapoda: Parastacidae) in southeastern Australia: electrophoretic, morphological and habitat variation *Australian Journal of Zoology* in press.
- Campbell, N.J.H., 1990. *An electrophoretic project on Euastacus armatus and Euastacus bispinosus*. Unpublished report, Zoology Department, University of Adelaide.
- Campbell, N.J.H., Geddes, M.C. and Adams, M., 1994. Genetic variation in yabbies *Cherax destructor* and *C. albidus* (Crustacea: Decapoda:

- Parastacidae) indicates the presence of a single, highly substructured species. *Australian Journal of Zoology* 42: 745–760.
- Clark, E., 1936. The freshwater and land crayfishes of Australia. *Memoirs of the National Museum of Victoria* 10: 5–58.
- Clark, E., 1937. The life history of the Gippsland crayfish. *The Australian Museum Magazine* 6: 186–192.
- Clark, E., 1941. Revision of the genus *Euastacus* (crayfishes, family Parastacidae), with notes on the distribution of certain species. *Memoirs of the National Museum of Victoria* 12: 7–30.
- Felsenstein, J. 1982. Numerical methods for inferring evolutionary trees. *Quarterly Review of Biology* 57: 379–404.
- Hamr, P., 1992. A revision of the Tasmanian freshwater crayfish genus *Astacopsis* Huxley (Decapoda: Parastacidae). *Papers and Proceedings of the Royal Society of Tasmania* 126: 91–94.
- Hedgecock, D., Tracey, M. L. and Nelson, K., 1982. Genetics. Pp. 285–403 in: Abele, L.G. (ed.), *The biology of Crustacea. Volume 2, embryology, morphology and genetics*. Academic Press: New York.
- Honan, J.A. and Mitchell, B.D., 1995. Reproduction of *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and trends in reproductive characteristics of freshwater crayfish. *Journal of Marine and Freshwater Research* 46: 485–499.
- Horwitz, P., 1988. Sea level fluctuations and the distributions of some freshwater crayfishes of the genus *Engaeus* (Decapoda: Parastacidae) in the Bass Strait area. *Australian Journal of Marine and Freshwater Research* 39: 427–502.
- Horwitz, P., 1990a. *The conservation status of Australian freshwater Crustacea: with a provisional list of threatened species, habitats and potentially threatening processes*. Report Series No.14. Australian National Parks and Wildlife Service: Canberra.
- Horwitz, P., 1990b. A taxonomic revision of species in the freshwater crayfish genus *Engaeus* Erichson (Decapoda : Parastacidae). *Invertebrate Taxonomy* 4: 427–614.
- Horwitz, P., 1995. *A preliminary key to the species of Decapoda (Crustacea: Malacostraca) found in Australian inland waters*. Identification Guide No. 5. Co-operative Research Centre for Freshwater Ecology: Albury.
- Horwitz, P., Adams, M. and Baverstock, P., 1990. Electrophoretic contributions to the systematics of freshwater crayfish genus *Engaeus* Erichson (Decapoda: Parastacidae). *Invertebrate Taxonomy* 4: 615–641.
- Lintermanns, M. and Rutzou, T., 1991. *The status, distribution and management of the Murray crayfish Euastacus armatus in the Australian Capital Territory*. ACT. Research Report 6. Department of Environment, Lands and Planning, ACT Parks and Conservation Service.
- Mayr, E., 1963. *Animal species and evolution*. Harvard University Press: Cambridge.
- Morgan, G. J., 1983. *A taxonomic revision of the freshwater crayfish genus Euastacus Clark (Decapoda: Parastacidae)*. Unpublished Ph. D. Thesis, Monash University.
- Morgan, G.J., 1986. Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from Victoria. *Memoirs of the Museum of Victoria* 47: 1–57.
- Morgan, G.J., 1988. Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from Queensland. *Memoirs of the Museum of Victoria* 49: 1–49.
- Morgan, G.J., 1989. Two new species of the freshwater crayfish *Euastacus* Clark (Decapoda: Parastacidae) from isolated high country of Queensland. *Memoirs of the Queensland Museum* 27: 555–562.
- Mulley, J.C. and Latter, B.D.H., 1980. Genetic variation and evolutionary relationships within a group of 13 species of penaeid prawns. *Evolution* 34: 904–916.
- Olszewski, P., 1980. *A salute to the humble yabby*. Angus and Robertson: Sydney.
- Patak, A. and Baldwin, J., 1994. Electrophoretic and immunochemical comparisons of haemocyanins from Australian fresh-water crayfish (Family Parastacidae): Phylogenetic implications. *Journal of Crustacean Biology* 4: 528–535.
- Nei, M., 1978. Estimates of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583–590.
- Nelson, K. and Hedgecock, D., 1980. Enzyme polymorphism and adaptive strategy in the decapod crustacea. *American Naturalist* 116: 238–280.
- Riek, E.F., 1956. Additions to the Australian freshwater crayfish. *Records of the Australian Museum* 24: 1–6.
- Riek, E.F., 1969. The Australian freshwater crayfish (Crustacea: Decapoda: Parastacidae). With description of new species. *Australian Journal of Zoology* 17: 855–918.
- Richardson, B.J., Baverstock, P.R. and Adams, M., 1986. *Allozyme electrophoresis. A handbook for animal systematics and population studies*. Academic Press: Sydney.
- Sneath, P.H.A. and Sokal, R.R., 1973. *Numerical taxonomy: the principles and practice of numerical classification*. Freeman: San Francisco.
- Swain, R., Richardson, A.M.M. and Hortle, M., 1982. Revision of the Tasmanian freshwater crayfish genus *Astacopsis* Huxley (Decapoda: Parastacidae). *Australian Journal of Marine and Freshwater Research* 33: 699–709.
- Swofford, D.L. and Selander, R.B., 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *Journal of Heredity* 72: 281–283.
- Thorpe, J.P., 1982. The molecular clock hypothesis: biochemical evolution, genetic differentiation

- and systematic. *Annual Review of Ecology and Systematics* 13: 139-168.
- Tracey, M.L., Nelson, K., Hedgecock, D., Shleser, R.A. and Pressick, M.L., 1975. Biochemical genetics of lobsters: genetic variation and the structured of American lobster (*Homarus americanus*) populations. *Journal of the Fisheries Research Board of Canada* 32: 2091-2101.
- Zeidler, W. and Adams, M., 1990. Revision of the Australian crustacean genus of freshwater crayfish *Gramastacus* Riek (Decapoda: Parastacidae). *Invertebrate Taxonomy* 3: 913-924.

DIVERSITY AND BIOGEOGRAPHY OF AUSTRALIAN MILLIPEDES (DIPLOPODA)

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Abstract

Black, D.G., 1997. Diversity and biogeography of Australian millipedes (Diplopoda). *Memoirs of the Museum of Victoria* 56(2): 557-561.

Twenty families of millipedes, representing nine orders, have been recorded from Australia. Three of these families and one of the orders are introduced. The greatest diversity is found east of the Great Dividing Range and in the south-east, including Tasmania. Approximately 250 native species have been described, probably representing only 10-20% of the actual number. Large areas of Australia, such as the north-west and west central coast, have yet to be adequately surveyed. Lack of detailed taxonomic and biological information precludes use of Australia's diverse millipede fauna for environmental management purposes.

Introduction

The millipede fauna of Australia is rich but largely unknown. As detailed below, nine of the 15 orders recognised in the world fauna (Hoffman, 1979) and 20 of the approximately 100 families (Hoffman, 1982) have been recorded from Australia. Three of the 20 families and one of the nine orders have been introduced since European settlement. P.M. Johns (pers. comm.) estimates that there are at least 2000 native species, about eight times the present known fauna. The majority of the undescribed species are small, inconspicuous soil and litter dwellers.

The aims of the present work were fourfold:

1. to briefly summarise the history of Australian millipede studies;
2. to give an overview of the taxonomic and morphological diversity of Australian millipedes at the order and family levels;
3. to document the geographical distributions of millipede orders and families regionally within Australia; and
4. to identify the major gaps in our present knowledge of the Australian millipede fauna.

Distributional records are based on data gleaned from specimen material lodged in all of the major museums in Australia, supplemented with records from collections made by the author and the personal research collections of R. Mesibov in Tasmania and J. Majer in Western Australia.

Millipede studies in Australia

Prior to about 1990 there were no millipede

taxonomists working within Australia. All taxonomic descriptions of Australian millipedes published before the 1990s had been prepared by European and North American specialists. Many of the specimens on which these works were based were collected during major expeditions to Australia early this century (Attems, 1911; Verhoeff, 1924). No attempt had been made, however, to characterise the nature of the fauna as a whole. Modern millipede studies began after the visit in 1980 of C.A.W. Jeekel, an eminent European systematist. In reporting this visit, Jeekel (1981) summarised the state of taxonomic knowledge of eastern Australian millipedes and documented zoogeographic distributions of higher taxa. His summary is, and will continue to be an invaluable reference for all subsequent millipede studies in this country.

In the 1980s, most published accounts dealing with Australian Diplopoda by local researchers concerned the ecology and control of the introduced *Ommatoiulus moreletii* Lucas, 1860 (the Black Portuguese Millipede). The research was concentrated in South Australia, where localised outbreaks of this nuisance pest were considered serious enough to have warranted considerable efforts in a search for a biological control agent. The search was carried out both in the area of origin of the species (Iberia) and in south-eastern Australia, and resulted in the importation of a parasitic fly from Portugal and the identification of a nematode parasitic in Australian millipedes (Baker, 1985a, b; Bailey, 1989; Shulte, 1989). Possible interactions between *O. moreletii* and native millipede species were investigated as an honours project at Flinders University in Adelaide (Griffin and Bull, 1995).

Other applied work on millipedes in Australia has dealt with the ecology of the pincushion millipede *Unixenus mjobergi* (Verhoeff, 1924) in the Pilbara region of Western Australia. Like *O. moreletii* this species also becomes a nuisance when it invades townships in the hundreds of thousands after rain (Burt, 1984; Koch, 1985).

Australian species of the order Chordeumatida (Craspedosomatida) have received recent attention (Golovatch, 1986; Mauriès, 1987; Shear and Mesibov, 1994, 1995), after first having been mentioned as being present in Australia by Jeekel (1981). This order is well represented in Australia, but all species are cryptic litter dwellers. The fact that it is only now being well documented illustrates the embryonic state of our knowledge of Australian millipedes generally.

Studies by resident Australian taxonomists have only begun in the last five years. R. Mesibov (Queen Victoria Museum and Art Gallery) has contributed to works on the Tasmanian Chordeumatida (Shear and Mesibov, 1994, 1995) and is investigating the systematics of the Tasmanian Dalodesmidae (Polydesmida) and the zoogeography of all Tasmanian millipedes. The author has undertaken revisions of genera in two Australian families, Siphonotidae (Polyzoniida) and Siphonophoridae (Siphonophorida), and is conducting a family level review and producing a key to the millipede families occurring in Australia.

Recent investigations of cave millipedes at Cape Range and Barrow Island, Western Australia, were initiated by W. Humphreys at the Western Australian Museum (Humphreys and Shear, 1993; Hoffman, 1994). Allozyme electrophoresis carried out on cave populations of the polydesmidan *Stygiochiropus* spp. from Cape Range (Humphreys and Shear, 1993) is one of the few examples of a molecular approach to millipede systematics in the literature.

Taxonomic and morphological diversity

Orders and families of Australian millipedes are listed in Table 1. Omitted from this table are the introduced taxa including the order Julida (families Julidae and Blaniulidae) and the Polydesmidae of the order Polydesmida, leaving eight orders and 17 families. Only one family, Peterjohnsiidae, is known to be endemic (Mauriès, 1987). The family list in Table 1 is based primarily on Jeekel (1981), Hoffman (1982) and the unpublished work of P.M. Johns. Harvey and Yen (1989) provide a very useful illustrated

key for identification of millipede material to order level.

The pincushion millipedes (Polyxenida) are atypical, being very small (generally less than 5 mm in length), extremely setose and able to withstand much drier conditions than most other Diplopoda.

Pill Millipedes (Sphaerotheriida) are inhabitants of wet eucalypt forest and rainforest. Since rainforest invertebrates have been much better collected in Australia than those from many other habitat types, the systematics of the Australian pill millipedes is probably better known than that of any other order.

The orders Polyzoniida and Siphonophorida are known as 'sucking millipedes' and show a reduction in mouthparts which is much more pronounced in the latter. Both groups are primarily wet forest millipedes. They are obviously not typical macrodetritivores, given the structure of their mouthparts, but what they do eat is unknown.

The Chordeumatida are small litter dwellers found in wet forest. Members of the two families found in Australia can be distinguished from other millipedes by the occurrence on each body segment of six dorsal macrosetae.

The most taxonomically diverse of the millipede orders in Australia is Polydesmida. The Paradoxosomatidae is the most speciose of all the native millipede families and paradoxosomatids are common in most forest and woodland habitats. Dalodesmidae are common in the east and south-west, and are particularly well represented in Tasmania. Members of the families Haplodesmidae and Pyrgodesmidae are difficult to distinguish from one another. They are small, highly sculptured and rigid-bodied animals, widespread in soil and litter. Very little is known about them in Australia, and there may be many undescribed species. At least one species of the family Polydesmidae, *Brachydesmus superus* Latzel, 1884 has been introduced to Tasmania (R. Mesibov, pers. comm.). The occurrence of this or other introduced Polydesmida elsewhere in Australia has not been reported.

Along with the introduced Julida, the last two orders in Table 1 are collectively known as 'juliform', which refers to the general body shape. Australian species of Julida are introduced. Most are restricted to metropolitan areas in southern Australia, but *Ommatoiulus moreletii* has made substantial inroads into dry native bush around the cities. The three families of Spirobolida in Australia are typically found in

Table 1. Regional distributions of Australian millipede families, excluding those introduced. P = present (recorded from that region); Qld = Queensland, NSW/Vic. = New South Wales and Victoria, Tas = Tasmania, NT = Northern Territory, SA = South Australia, Upper WA = upper Western Australia, Lower WA = lower Western Australia. Boundaries are approximate, based on divisions shown in Figure 2.

Taxon (Orders in caps)	Qld	NSW/ Vic.	Tas.	NT	SA	Upper WA	Lower WA
POLYXENIDA							
Synxenidae	P	P			P	P	P
Polyxenidae	P	P	P	P	P	P	P
Lophoproctidae	P					P	
SPHAEROTHERIIDA							
Sphaerotheriidae	P	P	P				P
SIPHONOPHORIDA							
Siphonophoridae	P	P		P			
POLYZONIIDA							
Siphonotidae	P	P	P		P	P	P
CHORDEUMATIDA							
Peterjohnsiidae	P	P	P				
Metopidiotrichidae	P	P	P				P
POLYDESMIDA							
Paradoxosomatidae	P	P	P	P	P	P	P
Dalodesmidae	P	P	P				P
Haplodesmidae and Pyrgodesmidae	P	P	P	P		P	P
SPIROSTREPTIDA							
Cambalidae	P	P	P				
Iulomorphidae	P	P	P	P	P	P	P
SPIROBOLIDA							
Rhinocricidae	P	P					
Pachybolidae	P	P		P	P	P	
Spirobolellidae	P	P					

rotten logs or litter of wet forest in the north of the continent. The two families of Spirostreptida are widespread, with many species adapted to drier conditions than are suitable for other millipedes. They are conspicuous components of the forest floor fauna, being found commonly in litter, rotten wood and under bark at the bases of trees.

Distributions of orders and families

Table 1 lists the distributions of the orders and families of millipedes found in Australia within six arbitrary divisions of the continent (Tasmania constituting a seventh region). The three introduced families have been omitted from the compilation. The table provides an overview of the diversity of Diplopoda at higher taxonomic levels in different areas of the country. Pyrgodesmidae and Haplodesmidae have been lumped

for this analysis because of difficulties in assigning species to one family or the other, giving maximum possible numbers of eight orders and 16 families.

As more collecting and survey work is carried out in more remote areas of Australia, the numbers in Table 1 are likely to increase considerably for the central and north-western divisions. However, our present knowledge of distributions suggests that the greatest millipede diversity occurs in eastern Australia. This dominance is almost certainly associated with the widespread occurrence of wet forest types east of the Great Dividing Range.

Gaps in knowledge

There is still a great deal of taxonomic work to be done on Australian millipedes. Polyxenida are common and widespread, but seldom collected

or recognised as millipedes. Large collections of material do exist, however, and the handful of species now known will no doubt increase to many times that number when Polyxenida eventually receive some attention. Sphaerotheriida are reasonably well known, and revisions of the Polyzoniida and Siphonophorida are being completed. Chordeumatida are currently receiving attention, but there are still many species to be described. Within the Polydesmida, the Dalodesmidae are currently being looked at, but the Paradoxosomatidae, the largest of all Australian families, are not being studied. The two families of tiny Polydesmida, Pyrgodesmidae and Haplodesmidae, are essentially unknown, although they are clearly well represented in Australia. Both orders of native juliforms, Spirobolida and Spirostreptida, are badly in need of work, with no resident expertise available.

As limited as our taxonomic knowledge is, our knowledge of the general biology of millipedes in Australia is even more sparse. Most of what little we do know was collected in the course of applied research into millipede control. Even basic topics have not been addressed, such as the relative importance of millipedes in nutrient turnover in forest ecosystems.

Conclusions

The taxonomic framework of millipede orders and families in Australia is fairly well known, but there is still much work needed below family level. The distributions of most species-level taxa are very poorly known, with the exception of those in the Tasmanian fauna. Basic information of this kind is required in order to make informed decisions about the conservation status of Australian millipedes, and at this point in time such assessment is quite impossible. Nevertheless, millipedes have the potential to be quite useful indicator taxa. In many forest and woodland habitats they are common and conspicuous, diverse, easily collected and sensitive to environmental perturbations. Given the taxonomic impediments involved, however, and the almost complete lack of knowledge of their general biology, millipedes cannot at this stage be recommended as 'environmental indicators' in Australia.

Acknowledgments

I am grateful to the collection managers and curators of myriapod collections at museums around Australia for making material available

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References

- Attems, C., 1911. Ergebnisse der Hamburger Sudwestaustralischen Forschungreise 1905. Myriopoda. *Die Fauna Sudwestaustralischens* 3(6): 145–204.
- Bailey, P.T., 1989. The millipede parasitoid *Pelidnota nigripennis* (F.) (Diptera: Sciomyzidae) for the biological control of the millipede *Ommatoiulus moreletii* (Lucas) (Diplopoda: Julida: Julidae) in Australia. *Bulletin of Entomological Research* 79: 381–391.
- Baker, G.H., 1985a. Parasites of the millipede *Ommatoiulus moreletii* (Lucas) (Diplopoda: Julidae) in Portugal, and their potential as biological control agents in Australia. *Australian Journal of Zoology* 32: 811–822.
- Baker, G.H., 1985b. The distribution and abundance of the Portuguese millipede *Ommatoiulus moreletii* (Diplopoda: Julidae) in Australia. *Australian Journal of Ecology* 10: 249–259.
- Burt, J., 1984. Report on the research of the pincushion millipede, *Unixenus mjobergi* (Verhoeff, 1924), at Tom Price, in the Pilbara of Western Australia. Western Australian Department of Agriculture.
- Golovatch, S.I., 1986. The first Chordeumatida (Diplopoda) from Tasmania, with the description of a new genus and three new species. *Zoologisches Jahrbuch, Systematisches Teil* 113: 251–264.
- Griffin, T.T. and Bull, C.M., 1995. Interactions between introduced and native millipede species in South Australia. *Australian Journal of Zoology* 43: 129–140.
- Harvey, M.S. and Yen, A.L., 1989. *Worms to Wasps; An Illustrated Guide to Australia's Terrestrial Invertebrates*. Oxford University Press: Melbourne.
- Hoffman, R., 1979. *Classification of the Diplopoda*. Museum d'Histoire Naturelle: Genève.
- Hoffman, R., 1982. Diplopoda. Pp. 689–724 in: Parker, S.P. (ed.), *Synopsis and classification of living organisms*. McGraw-Hill: New York.
- Hoffman, R.L., 1994. Studies on spiroboloid millipeds. XVIII. *Speleostrophus nesiotis*, the first known spiroboloid millipede, from Barrow Island, Western Australia (Diplopoda: Pachybolidae: Trigonulinae). *Myriapodologica* 3(3): 19–24.
- Humphreys, W.F. and W.A. Shear, 1993. Troglolithic millipedes (Diplopoda: Paradoxomatidae) from semi-arid Cape Range, Western Australia: systematics and biology. *Invertebrate Taxonomy* 7: 73–195.

- Jeekel, C.A.W., 1981. Australian Expedition 1980; legit C.A.W. Jeekel and A.M. Jeekel-Rijvers. List of collecting stations, together with general notes on the distributions of millipedes in eastern Australia and Tasmania. *Verslagen en Technische Gegevens, Instituut voor Taxonomische Zoologie, Universitat Amsterdam* 30: 1-59.
- Koch, L.E., 1985. Pincushion millipedes (Diplopoda: Polyxenida): Their aggregations and identity in Western Australia. *Western Australian Naturalist* 16(2/3): 30-31.
- Mauriès, J-P., 1987. Craspedosomid millipedes discovered in Australia: *Reginaterreuma*, *Neocambrisoma* and *Peterjohnsia*, new genera (Myriapoda: Diplopoda: Craspedosomida). *Memoirs of the Queensland Museum* 25: 107-133.
- Shear, W.A. and Mesibov, R., 1994. Australian chordeumatidan millipedes. I. New observations on the genus *Peterjohnsia* Mauriès, with the description of a new species from Tasmania (Diplopoda, Chordeumatida, Peterjohnsiidae). *Invertebrate Taxonomy* 8: 535-544.
- Shear, W.A. and Mesibov, R., 1995. Australian chordeumatidan millipedes. II. A new species of *Reginaterreuma* Mauriès from Tasmania (Diplopoda, Chordeumatida, Metopidiotrichidae). *Myriapodologica* 3(8): 71-77.
- Shulte, F., 1989. The association between *Rhabditis necromena* Sudhaus & Shulte, 1989 (Nematoda: Rhabditidae) and native and introduced millipedes in South Australia. *Nematologica* 35: 82-89.
- Verhoeff, K.W., 1924. Results of Dr. E. Mjöberg's scientific expeditions to Australia 1910-1913, 34. Myriapoda: Diplopoda. *Arkiv foer Zoologi* 16(5): 1-142.

A ZOOGEOGRAPHICAL SINGULARITY AT WEAVERS CREEK, TASMANIA

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Abstract

Mesibov, R., 1997. A zoogeographical singularity at Weavers Creek, Tasmania. *Memoirs of the Museum of Victoria* 56(2): 563–573.

A narrow landscape zone containing the range boundaries of at least six widespread millipede species and two widespread centipede taxa has been mapped at Weavers Creek, near Launceston in northern Tasmania. Two other, geographically restricted millipede species are unusually abundant in the zone. Although the zone coincides with a broad ecotone between dry and wet eucalypt forest, its existence is most plausibly explained as the result of interspecific competition and historical factors. Weavers Creek is neither a 'centre of endemism' for litter invertebrate diversity nor the site of unusual forest habitats. The area is nevertheless of considerable conservation significance because of the insights it affords into ecological parapatry and local-scale invertebrate evolution.

Introduction

The East Tamar Break in north-east Tasmania is a c. 50 km-long faunal boundary respected by a range of litter invertebrates (Mesibov, 1994a). In this article I report progress in mapping millipede distributions near the southern end of the East Tamar Break, where a boundary c. 5 km wide passes through a large block of lightly disturbed native forest in the Weavers Creek catchment, south-west of Mt Barrow. This portion of the Break, it is argued, should be conserved as a field laboratory for studies of parapatry and invertebrate evolution.

Methods

Between December, 1991 and December, 1995 I searched for polydesmidan millipedes at 154 sites within a 30 × 30 km study area just east of Launceston (Figs 1 and 2). Millipedes were hunted in rotting logs, in and under leaf litter and stones, and in the top layers of richly organic soil. Hand-collecting is a more efficient method for sampling millipedes than pitfall-trapping (Mesibov et al., 1995) and is particularly well-suited to sampling in small remnants of native bush, where millipedes may be concentrated in a few square metres of suitable habitat. My by-catch included chordeumatidan and polyzoniidan millipedes, centipedes and velvet worms. All collections have been lodged at the Queen Victoria Museum and Art Gallery (QVMAG) in Launceston. Specimens of the undescribed millipedes and centipedes referred to in this paper have been registered as sorted taxa (e.g., *Lisso-desmus* n. sp. E1 pending further taxonomic study.

Geographical overview

Mt Barrow stands at the high, eastern edge of a tilted and block-faulted sheet of Jurassic dolerite (Longman, 1966). Drainage west of Mt Barrow is partly controlled by north-north-westerly-trending faults, as exemplified by Weavers Creek and the St Patricks River within the study area (Fig. 3). The narrow rectangle in Fig. 3 was drawn perpendicular to the fault trend, and mid-point elevations were noted (from 1:25000 topographic maps) on 1 km-wide strips across the

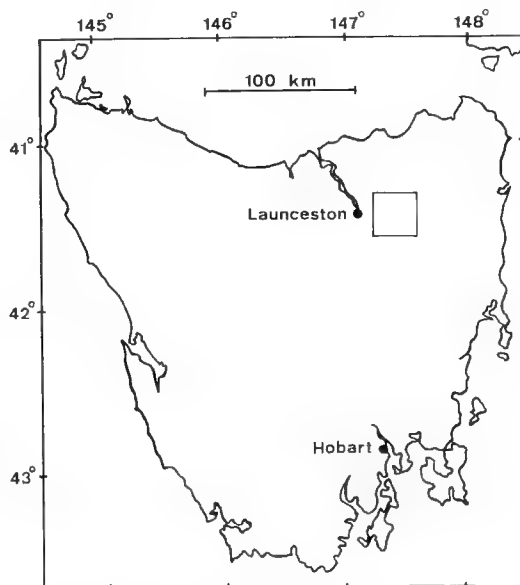


Figure 1. Location of the 30 x30 km study area, just east of Launceston.

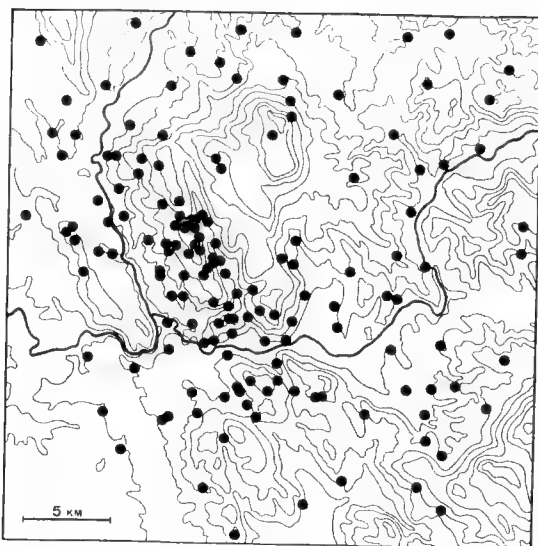


Figure 2. Distribution of sampling sites in the study area (to 8 December 1995).

width of the rectangle every 250 m from its western end. The resulting elevation profile (Fig. 4) clearly shows the step-faulted structure of the Weavers Creek area. For convenience in description I have given the name 'Weavers Ridge' to the long hill between Weavers Creek and the St Patricks River. At the southern end of Weavers Ridge, Weavers Creek abruptly abandons a major fault line and turns west to join the North Esk River (Fig. 3).

Early Tertiary deposits in the long basins between fault blocks in the Tamar area are generally flat-lying and unfaulted, indicating that faulting and tipping of the dolerite masses occurred prior to the early Tertiary (Longman, 1966). Minor eruptions of Tertiary basalt at Nunamara and Watery Plains are believed to have diverted the St Patricks and North Esk Rivers into their present courses (Longman, 1966), but the general structure of the landscape in the study area appears to have been stable through most of the Tertiary. Although Mt Barrow is not thought to have been glaciated during the Pleistocene (Caine, 1983), periglacial effects were severe and much of Weavers Ridge is mantled with frost-shattered dolerite debris and solifluction colluvium (Mesibov, unpublished observation).

The steep elevation gradient in Fig. 4 is paralleled by a steep gradient in annual rainfall (Fig. 5) and by a transition from dry eucalypt forest and woodland on the Tressick Hills (Fig. 4) to wet eucalypt forest on the western, lower slopes of Mt Barrow. A broad ecotone between dry and

wet eucalypt forest covers Weavers Ridge. In the general vicinity of Weavers Creek, all native plant cover is eucalypt forest apart from alpine scrub on Mt Barrow (treeline c. 1100 m) and riparian strips of *Nothofagus*-dominated rain-forest on the Creek itself and its tributaries on the Mt Barrow side. Very little of the steeper ground in the study area has been cleared for agriculture (Fig. 6), but grazing and frequent burning over the past 150 years have degraded the dry eucalypt forest on the Tressick Hills and the wooded hills south of the North Esk. The whole of the uncleared portion of the study area (apart from alpine scrubs and screes) was forested in pre-European times, and nearly all that forest has been selectively logged (in places repeatedly) and naturally regenerated. Small plantations of *Pinus radiata* and *Eucalyptus nitens* have been developed in recent years on non-rocky ground within the study area, but much of the uncleared land in Fig. 6 carried weed-free native forest in 1995, with a variably abundant litter fauna.

Distributions of polydesmidan millipedes

Polydesmidan or 'flat-backed' millipedes are the most species-diverse and abundant Diplopoda in Tasmania (Mesibov, 1994b). The most speciose local genus is *Lissodesmus* Chamberlin in the Dalodesmidae, with at least 25 Tasmanian and 3 Victorian species (Mesibov, in preparation). Several species of *Lissodesmus* in the study area are shallow-burrowing in soil and deep litter (Table 1). *L. adrianae* Jeekel, 1984 is a north-east Tasmanian endemic with a western range boundary at the East Tamar Break (Fig. 7) and an apparent preference for very moist microhabitats. The more ecologically tolerant *L. alisonae* Jeekel, 1984 (Table 1) has its eastern range boundary at the Break (Fig. 8). *Lissodesmus* n. sp. E1, a widespread eastern species, is parapatric with *L. alisonae* at the latter's southern limit (Figs. 8, 9) and overlaps fairly broadly with *L. adrianae* (Figs. 7, 9), although *adrianae*/E1 parapatry has been documented near Mt Horror and Rayners Hill in north-east Tasmania (Mesibov, unpublished observations). These three species of *Lissodesmus* meet at a distributional 'triple point' near the southern end of Weavers Ridge (Figs. 7, 8, 9).

Lissodesmus n. sp. NE1 and the unrelated dalodesmid *Tasmanodesmus hardyi* Chamberlin, 1920 are morphologically convergent (Table 1) and adapted for life in loose litter and cavities in rotting logs. *T. hardyi* is widespread in

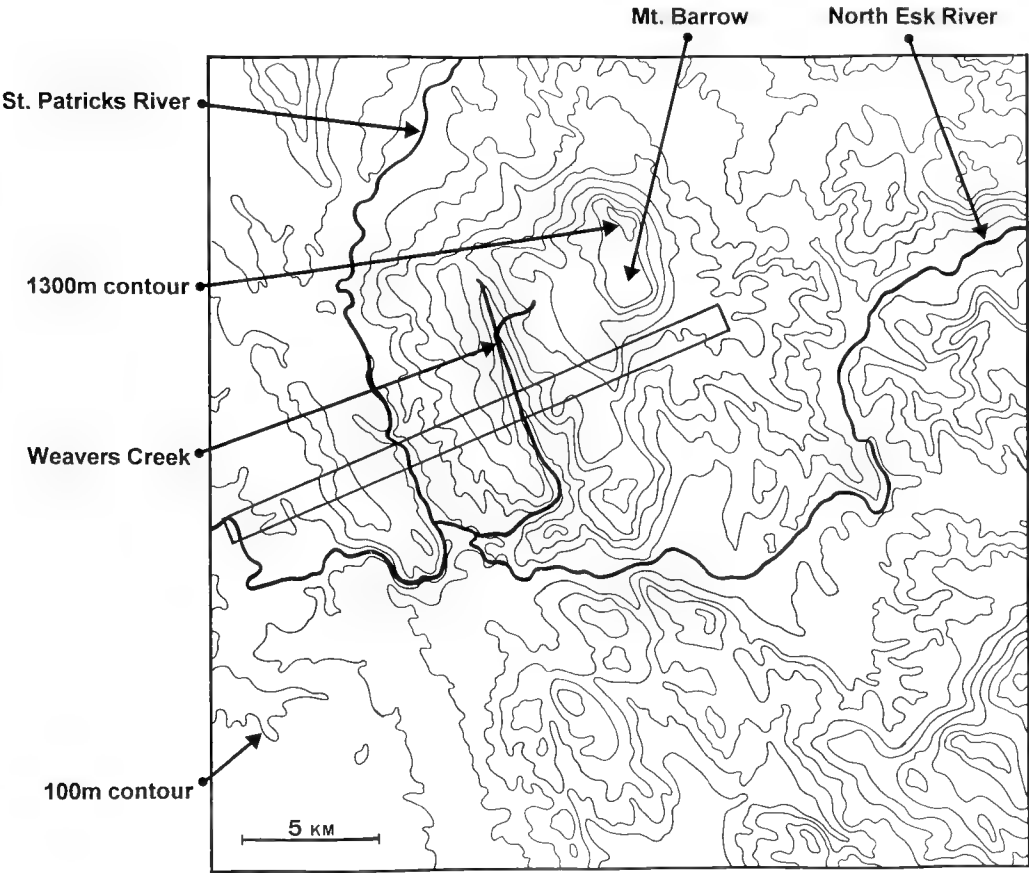


Figure 3. Features of the study area. St Patricks River and Weavers Creek are tributaries of the west-flowing North Esk River. Narrow rectangle defines the elevation transect in Fig. 4 (see text for details). Contour interval is 100 m.

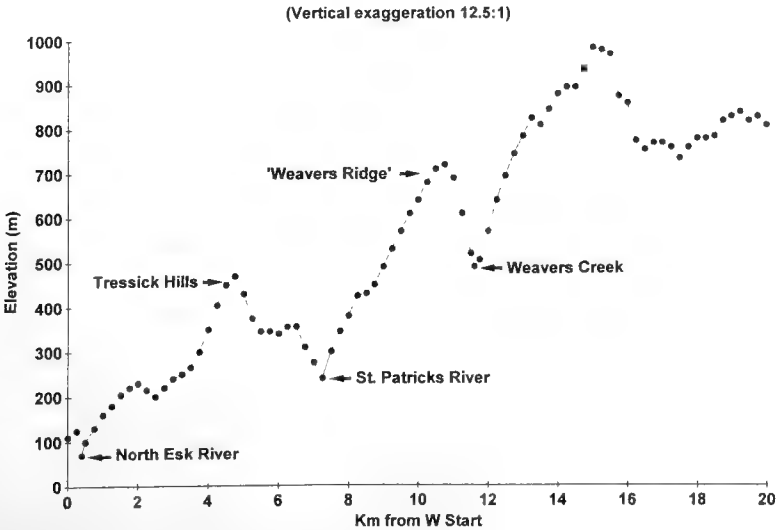


Figure 4. Elevation transect along narrow rectangle in Fig. 3 (see text for details).

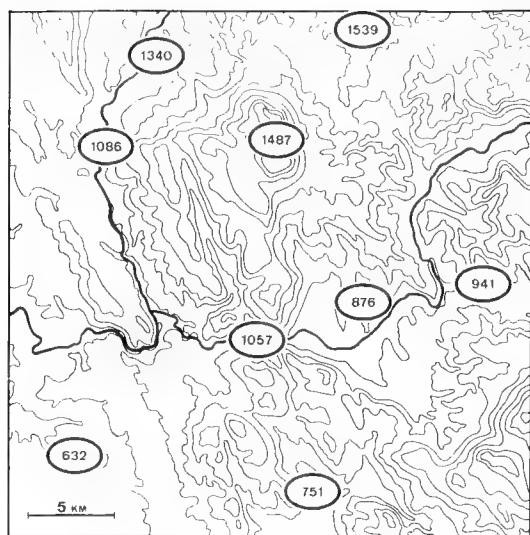


Figure 5. Annual rainfall in millimetres in the study area (data courtesy Bureau of Meteorology). Clockwise from the south, the stations and years of record are: '751', Deddington-Nile River (63 years); '632', Evandale-Ridgeside (58), '1086', combined Nunamara (15 and 30), '1340', St Patricks River (83), '1487', combined Mt Barrow (6 and 12), '1539', Diddleum Plains (33), '941', Blessington-Heathcote (22), '876', Burns Creek-Janefield (21), '1057', Musselsboro-Aplico (40).

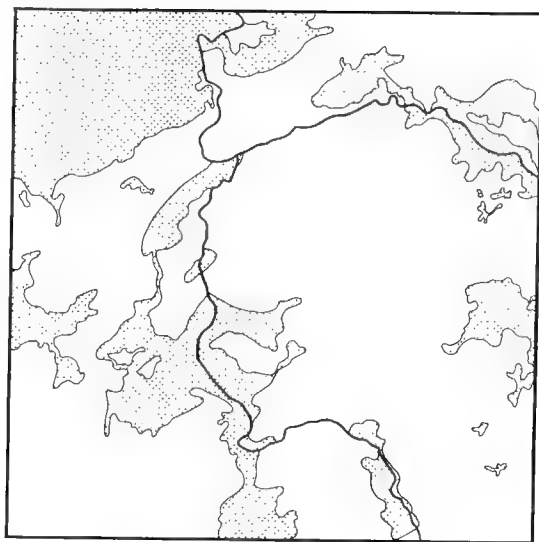


Figure 6. Extent of clearance for agriculture (stippled) in the study area, based on Landsat images (January, 1994). Apart from small areas of alpine vegetation, all uncleared land has tree cover. Woodland adjacent to cleared ground, especially in the south-west of the study area, has been degraded by grazing and frequent burning. A small and scattered proportion of the forested area (c. 10%) has been converted to plantations of non-native trees in recent years.

Tasmania (Fig. 10) while *Lissodesmus* n. sp. NE1 is a north-east Tasmanian endemic (Fig. 11). The two distributions abut at the East Tamar Break.

A sixth widespread polydesmidan occurring in the study area is a distinctive but undescribed paradoxosomatid (n. gen., n. sp.) found throughout much of eastern Tasmania (Fig. 12) in open forest, woodland and scrub, where it is sometimes day-active (Mesibov, unpublished observations). It has not been found east of the East Tamar Break in the study area (Fig. 12).

Two dalodesmids with restricted distributions also occur in the study area. The first is in an undescribed genus with three widely disjunct species in Tasmania (Mesibov, in preparation). This species, here called dalodesmid n. gen. 2, n. sp. 2, is a deep-burrowing form rarely seen in the litter layer; it is particularly abundant in the study area (Fig. 13) and persists in tiny bush remnants (<0.5 ha) on local farms. The second dalodesmid is *Lissodesmus* n. sp. NE3, known only from one site outside the study area but locally abundant at sites near Weavers Creek

(Fig. 14). *Lissodesmus* n. sp. NE3 is intermediate in sexual characters between *Lissodesmus* n. sp. E1 and *L. alisonae* and may represent a stabilised hybrid taxon (Mesibov, in preparation).

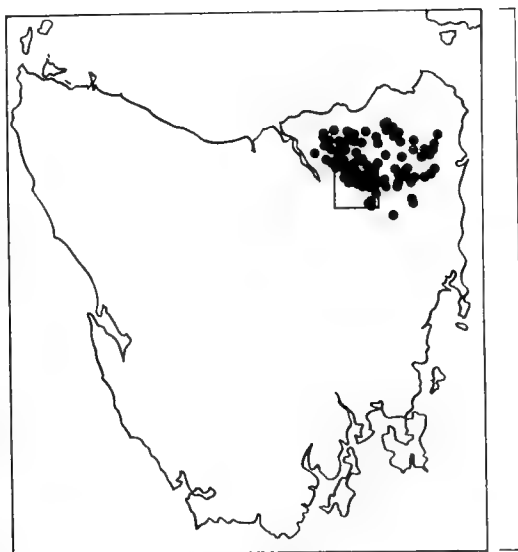
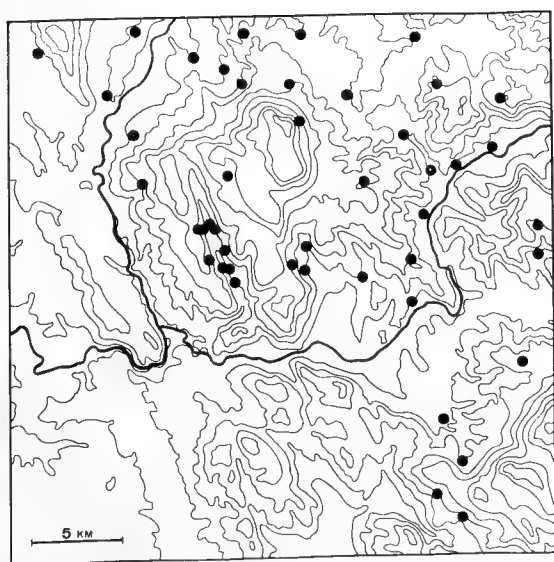
A consensus sketch of the East Tamar Break in the Weavers Creek area, drawn from the distributions just reported, is offered in Fig. 15. Range boundaries within this zone of overlap run from c. 300 to c. 700 m elevation, chiefly along Weavers Ridge in the broad dry/wet eucalypt ecotone. The south-western edge of the zone roughly coincides with the 1000 mm isohyet (Fig. 5).

Distributions of other litter invertebrates

To date, no litter macroinvertebrates other than millipedes and centipedes have been intensively mapped in the study area by specialist collectors, although snails, amphipods, isopods, spiders, harvestmen, carabid beetles and neanurid collembolans are all locally abundant. I am currently sorting the smaller Tasmanian Polydes-

Table 1. Some features of millipede species mapped in this article. (Rainfall ranges estimated from isohyet maps.)

Species	Elevation Range (m)	Rainfall Range (mm)	Characters	Microhabitat
<i>Lissodesmus adrianae</i>	60–1050	850–1700	15–20 mm long;	deep moist litter,
<i>Lissodesmus alisonae</i>	10–1010	650–1500	reduced paranota;	upper horizon of
<i>Lissodesmus</i> n. sp. E1	10–840	600–1100	lightly pigmented	organic-rich soil
<i>Lissodesmus</i> NE1	20–790	800–1700	25–30 mm; wide	loose moist litter,
<i>Tasmanodesmus hardyi</i>	10–1120	600–2000	paranota; long, thin legs; purple-brown pigmentation	cavities in moist rotting logs
paradoxosomatid, n. gen. n. sp.	50–1120	600–1100	20–25 mm; very reduced paranota; heavily sclerotised cuticle; dark brown or black	loose dry or wet litter; under bark and stones
dalodesmid, n. gen. 2, n. sp. 2	270–1000	700–1200	20–25 mm; very reduced paranota; heavily calcified cuticle; lightly pigmented	deeper layers of organic-rich soil, deep in wet rotting logs
<i>Lissodesmus</i> n. sp. NE3	350–710	700–1000	15 mm; partly reduced paranota; lightly pigmented	as <i>L. adrianae</i>

Figure 7. Distribution of *Lissodesmus adrianae* in the study area and Tasmania as a whole. Closely adjacent localities on the State map have been marked with a single dot. Localities are those known as of 8 December 1995.

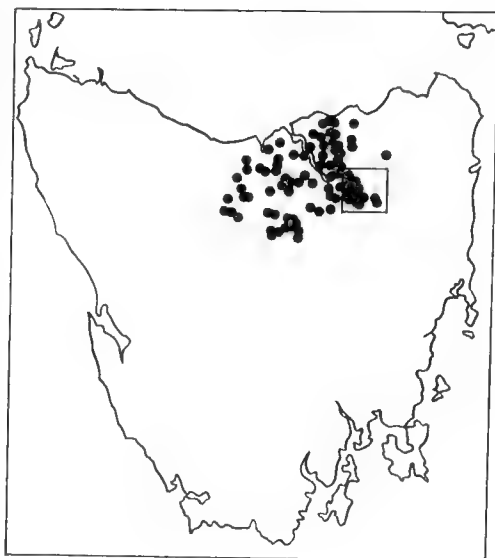
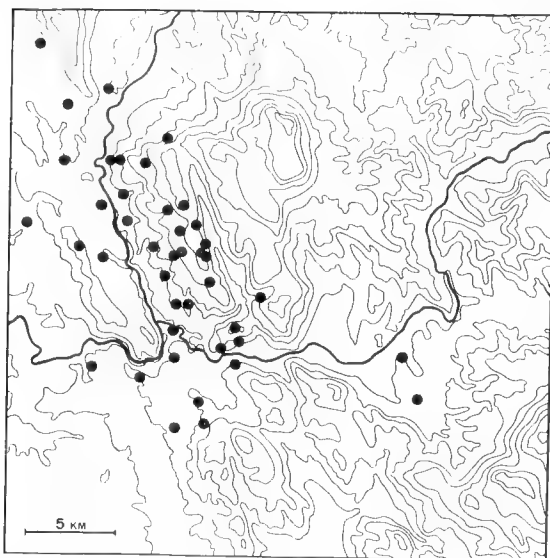


Figure 8. As Fig. 7, for *Lissodesmus alisonae*.

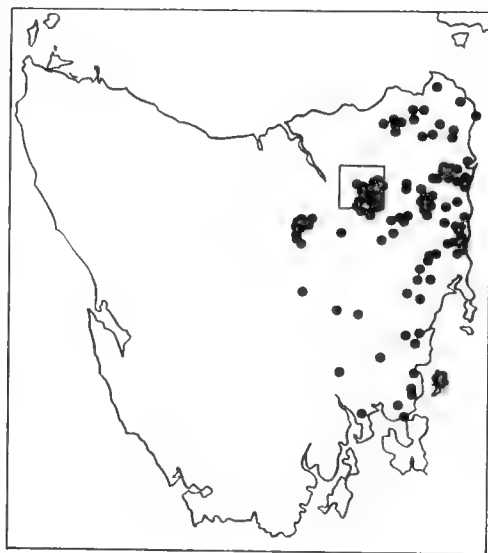
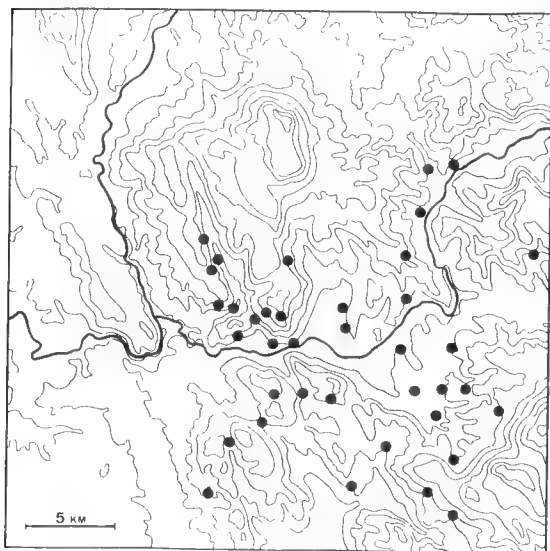


Figure 9. As Fig. 7, for *Lissodesmus* n. sp. E1.

mida to morphospecies and looking for additional distributional congruences in the study area. A preliminary sorting of geophilomorph centipedes in the genus *Tasmanophilus* is being carried out in collaboration with R.L. Jones (Kings Lynn, UK) and a distinctive new species with 41–45 leg pairs, here called *Tasmanophilus* n. sp., is known to be a north-east regional endemic (Fig. 16). All other local *Tasmanophilus* species (the *T. 'opinatus'* group) have 49 or more pairs of legs; their combined distributions in the study area are shown in Fig.

17. The overlap again appears to be concentrated on Weavers Ridge.

Why Weavers Creek?

It is unwise to assume that all the range boundaries concentrated in the Weavers Creek area are there for the same reason. The simplest explanation for the paradoxosomatid (n. gen., n. sp.) range limit is that this species prefers open forest, and that denser understorey vegetation on the Mt Barrow side of Weavers Creek is unfavourable habitat and a dispersal barrier.

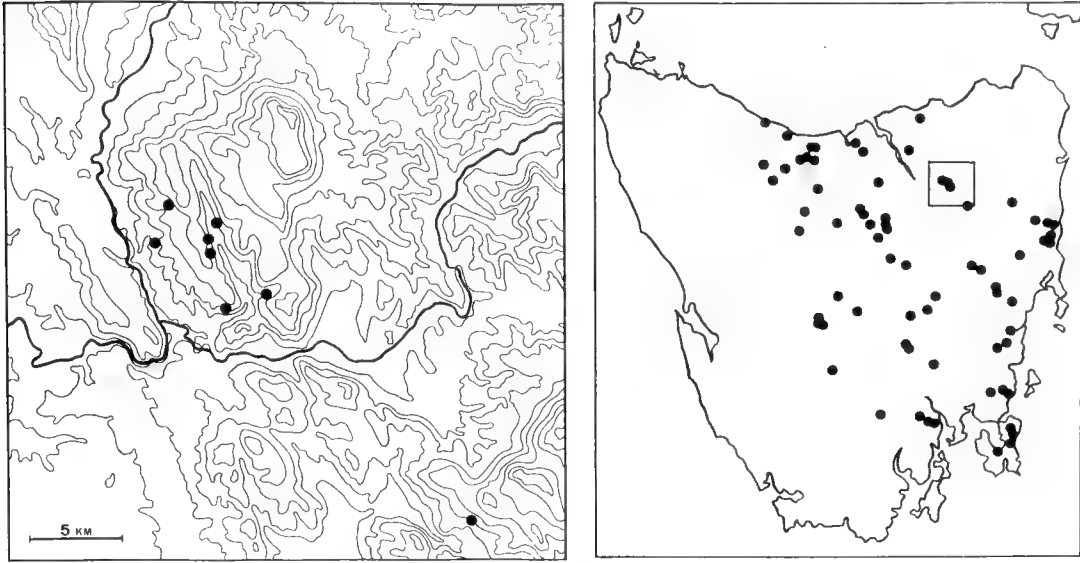


Figure 10. As Fig. 7, for *Tasmanodesmus hardyi*.

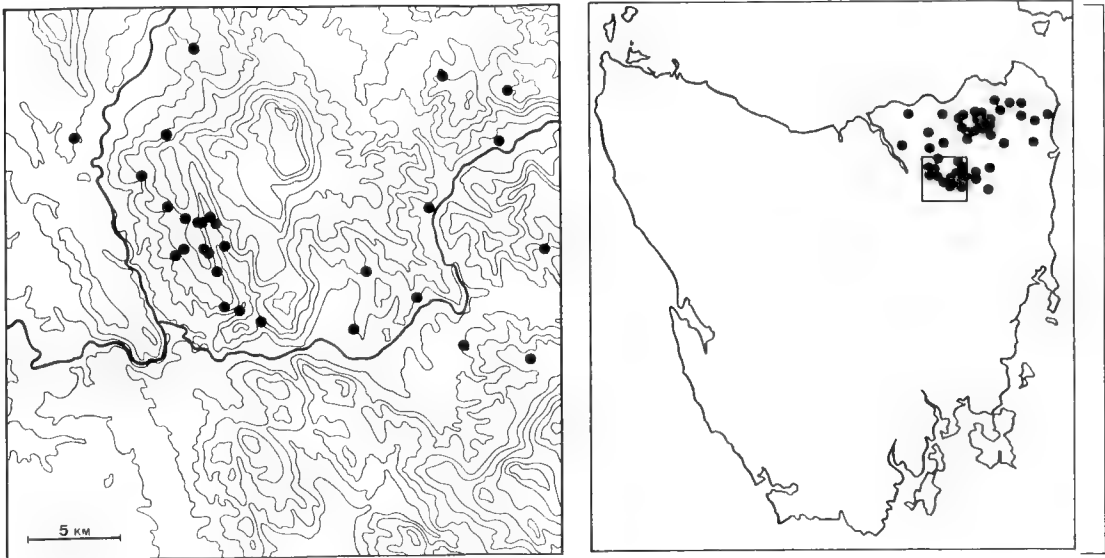


Figure 11. As Fig. 7, for *Lissodesmus* n. sp. NE1.

Habitat preference fails as an explanation for *Lissodesmus* and *Tasmanodesmus* parapatry, since the five species concerned are known to flourish in a wide variety of forest and scrub habitats across their respective ranges. It seems more likely that the parapatric species pairs compete in some way, and exclude each other from areas where either could exist in the absence of a competitor. Explanations of this kind have been advanced for parapatry in freshwater crayfish (Flynn and Hobbs, 1984) and frogs (Odendaal and Bull, 1982). A postglacial

origin for parapatry by secondary contact between subspecies has been suggested for the grasshopper *Chorthippus parallelus* in the Pyrenees (Cooper and Hewitt, 1993). Parapatry between less closely related millipedes in the Weavers Creek area may have arisen in the Holocene in a similar way, since the area experienced periglacial conditions in the late Pleistocene and probably lacked tree cover. On the other hand, geological evidence (see above) indicates that the general form of the landscape in the Weavers Creek area has changed little over

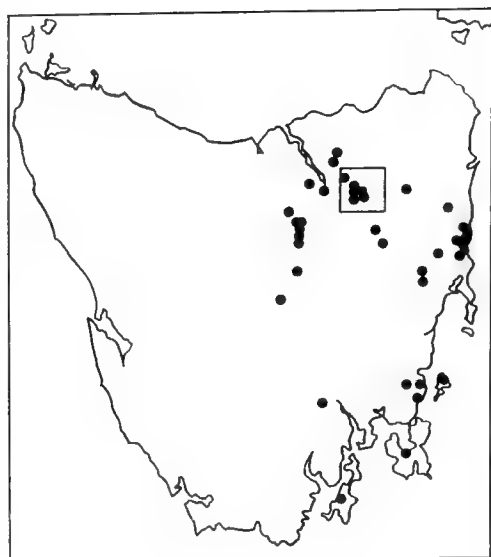
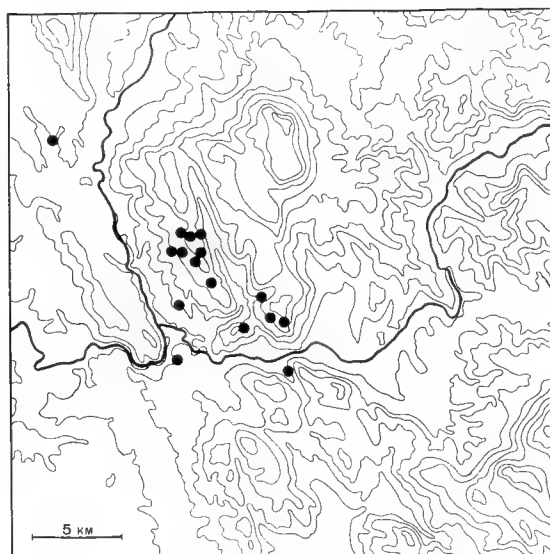


Figure 12. As Fig. 7, for paradoxosomatid n. gen., n. sp.

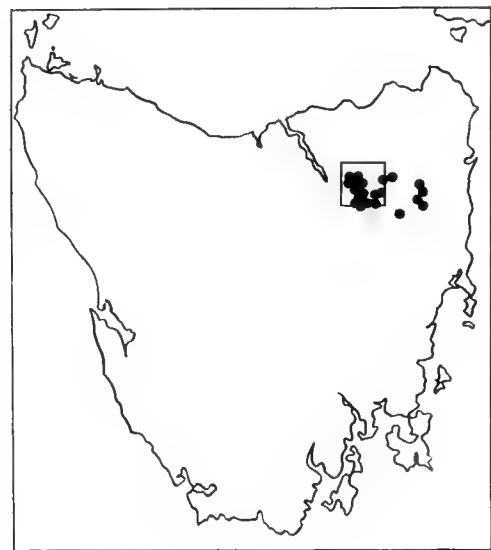
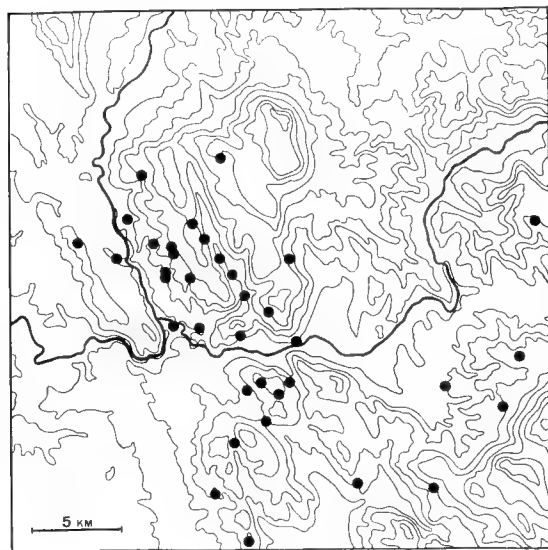


Figure 13. As Fig. 7, for dalodesmid n. gen. 2, n. sp. 2.

millions of years. Millipedes in the area may therefore have been parapatric well before the ice ages, and their parapatry may have been interrupted and re-established during glacial and interglacial times, respectively. This notion is in accord with the hypothesis that *Lissodesmus* n. sp. NE3 is a stabilised hybrid derived from a previous *alisonae*/E1 contact period, and now persisting as a relict at two disjunct locations in north-east Tasmania. Molecular phylogenetic studies of Tasmanian dalodesmids will shed light on these historical-biogeographi-

cal questions. Questions concerning the location of the Weavers Creek overlap zone — whether and in which direction it may be moving, and where it was in the Tertiary and Pleistocene interglacials — are unanswerable.

Conservation

The Weavers Creek section of the East Tamar Break is a remarkable biogeographical feature, but there is little else to recommend it as an area worthy of conservation. It is not known to

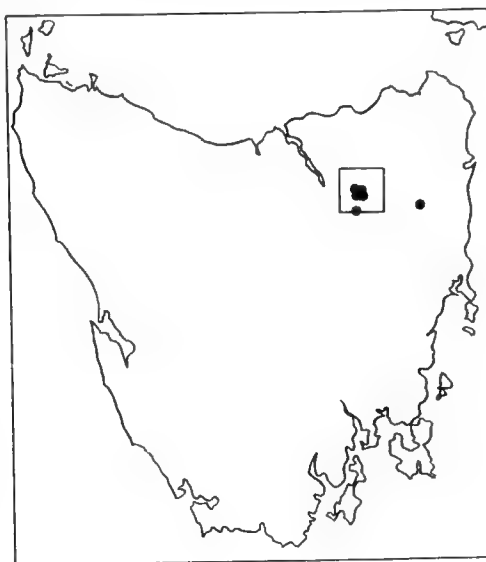
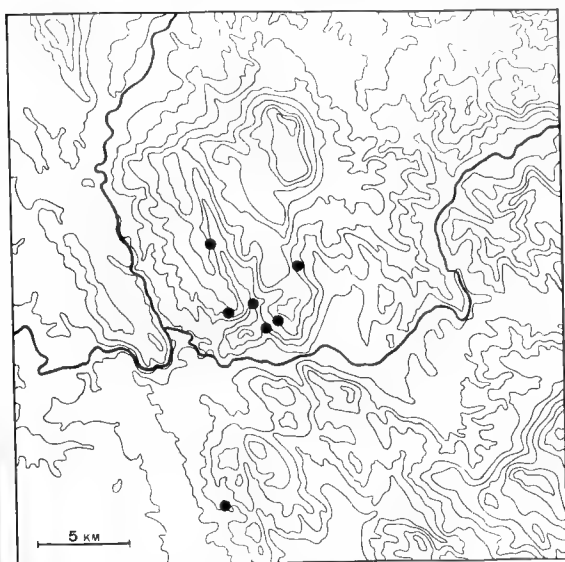


Figure 14. As Fig. 7, for *Lissodesmus* n. sp. NE3.

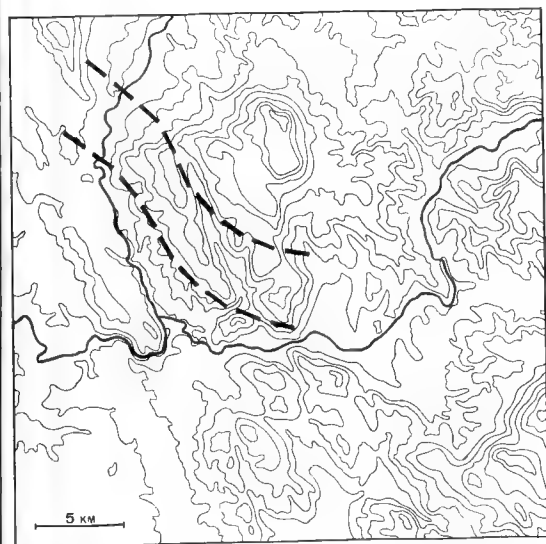


Figure 15. Approximate location of the East Tamar Break in the Weavers Creek area, as defined by millipede range boundaries

harbour a concentration of rare and unusual terrestrial invertebrates, the only rare species collected there to date being the millipede *Lissodesmus* n. sp. NE3. North-east of the area is the c. 2000 km² 'centre of endemism' known as Plomleys Island (Mesibov, 1994a), but the Weavers Creek overlap zone lies on its margin and at least one Plomleys Island endemic, the millipede *Gasterogramma* n. sp. 5, has not yet

been found in the Weavers Creek catchment. Forest vegetation in the zone is typical for the area. A 779 ha block of State forest at the southern end of Weavers Ridge is a proposed Forest Reserve (B. Farmer, Forestry Tasmania, pers. comm.), but the block was first selected as a Recommended Area for Protection because it is a regionally representative area of dry eucalypt forest (Brown and Hickey, 1990).

There is also little evidence that millipedes in the zone require special protection. It is no harder to find litter invertebrates, generally, in recently logged areas on Weavers Ridge than in adjoining unlogged forest. An intense wildfire in December, 1994 burned through most of the proposed Forest Reserve on Weavers Ridge, but the dry forest vegetation is recovering well and millipedes can still be found in the burned area. The 'robustness' of litter fauna on Weavers Ridge is almost certainly due to the extensive cover of dolerite debris; litter can accumulate in spaces between and below the rocks, and litter invertebrates can shelter there from fire and logging disturbance. In contrast, on the nearby Tressick Hills millipedes are more or less restricted to patches of rock-mantled ground, while sparsely grassed intervening areas are heavily disturbed by sheep. The rock cover on Weavers Ridge also provides insurance against clearance for agriculture and forest plantations.

It is nevertheless possible that non-litter species occur in tight parapatry on Weavers Ridge, and for this reason alone there is a case to

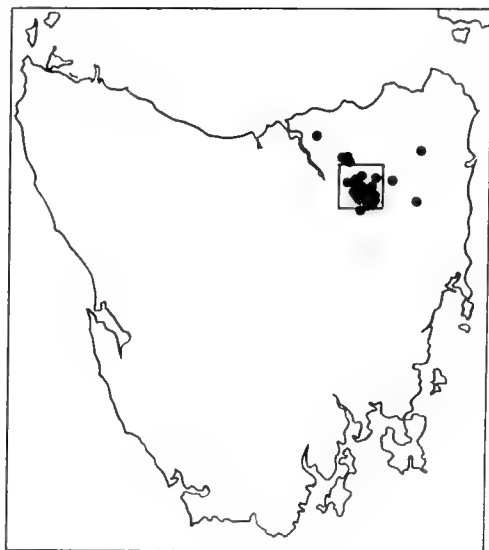
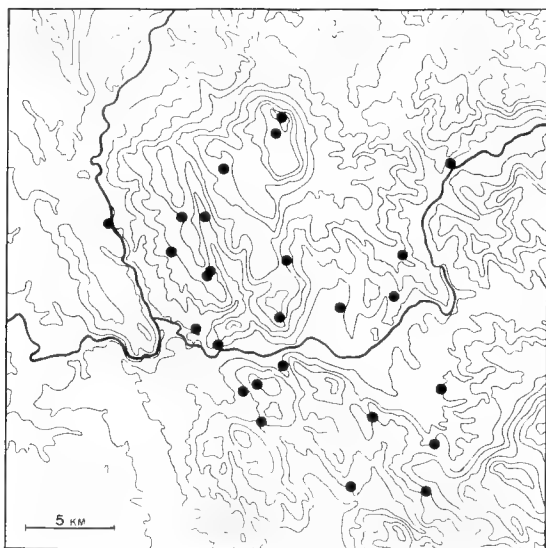


Figure 16. As Fig. 7, for *Tasmanophilus* n. sp.

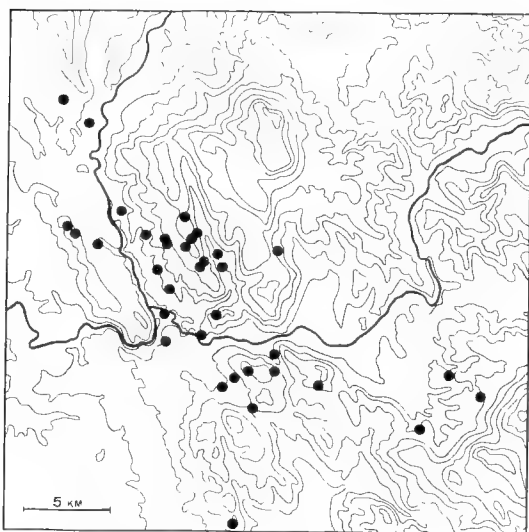


Figure 17. Distribution of *Tasmanophilus* 'opinatus' group (see text) in the study area.

be made for special recognition and gentle handling of the Weavers Creek area. Bull (1991) has suggested that parapatry may have been a more common phenomenon before natural habitats were fragmented by clearance. In Tasmania, the Weavers Creek parapatric zone is the narrowest so far discovered, and its location in lightly disturbed forest increases its value for field studies of the mechanisms by which parapatric bound-

aries are maintained. The tenure of the area concerned is almost entirely State forest. Local Forestry Tasmania staff have been briefed on sampling results and are prepared to consider special management of a zoogeography study area at Weavers Creek (B. Farmer, pers. comm.). To upgrade the conservation status of the area, sampling and field research results for invertebrate groups other than millipedes and centipedes are needed.

Acknowledgements

My field work in the Weavers Creek area has been generously supported by the Plomley Foundation. Brian Farmer and Paul Rosevear (Forestry Tasmania) provided maps, advice and logging history. Landsat images were made available by Ross Lincoln (Space Images, University of Tasmania). I am especially grateful to my wife, Catriona Moule, and Daniel Soccol (QVMAG) for assistance in the field.

References

- Brown, M. and Hickey, J., 1990. Tasmanian forest — genes or wilderness? *Search* 21: 86–87.
- Bull, C.M., 1991. Ecology of parapatric distributions. *Annual Review of Ecology and Systematics* 22: 19–36.
- Caine, N., 1983. *The mountains of northeastern Tasmania. A study of alpine geomorphology*. Bol-kema: Rotterdam.

- Cooper, S.J.B. and Hewitt, G.M., 1993. Nuclear DNA sequence divergence between parapatric subspecies of the grasshopper *Chorthippus parallelus*. *Insect Molecular Biology* 2: 185-194.
- Flynn, M.F. and Hobbs, H.H., 1984. Parapatric crayfishes in southern Ohio: evidence of competitive exclusion? *Journal of Crustacean Biology* 4: 382-389.
- Longman, M.J., 1966. *Geological survey explanatory report, one mile geological map series, K/55-7-39, Launceston*. Tasmania Department of Mines: Hobart.
- Mesibov, R., 1994a. Faunal breaks in Tasmania and their significance for invertebrate conservation. *Memoirs of the Queensland Museum* 36: 133-136.
- Mesibov, R., 1994b. Tasmania and its myriapods. *Bulletin of the British Myriapod Group* 10: 51-58.
- Mesibov, R., Taylor, R.J. and Brereton, R. N., 1995. Relative efficiency of pitfall trapping and hand-collecting from plots for sampling of millipedes. *Biodiversity and Conservation* 4: 429-439.
- Odendaal, F.J. and Bull, C.M., 1982. A parapatric boundary between *Ranidella signifera* and *R. riparia* (Anura: Leptodactylidae) in South Australia. *Australian Journal of Zoology* 30: 49-57.

THE BIODIVERSITY OF TERRESTRIAL FLATWORMS (TRICLADIDA: TERRICOLA) IN QUEENSLAND : A PRELIMINARY REPORT

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Abstract

Winsor, L., 1997. The biodiversity of terrestrial flatworms (Tricladida: Terricola) in Queensland: a preliminary report. *Memoirs of the Museum of Victoria* 56(2): 575-579.

Prior to this study of the Terricola in Queensland only nine species of terrestrial flatworms (land planarians) were reported from south and mid-east Queensland. Nothing was known of the flatworm taxa of the northern regions of the state. As a result of the study the known Queensland flatworm fauna has been increased over six fold. Eight genera and over 80% of the 62 species are new. Seven exotic species have been recorded from disturbed habitat. The flatworm fauna in the northern tropics exhibits high diversity and apparent endemicity in both the Rhynchodemidae and Geoplanidae, and shares some taxa with Indonesia and Irian-Jaya — Papua-New Guinea. It includes *Cotyloplana*, *Digonopyla* and *Dolichoplana* not previously recorded from the Australian mainland. The southern areas of the state are dominated by a less diverse geoplanid fauna with affinities with the south-eastern states and New Zealand. Threats to conservation include deforestation and destruction of remnant ground cover by humans and exotic animals.

Introduction

Terrestrial flatworms, also known as land planarians, are conspicuous carnivores of the Australian native forest cryptofauna. Generally regarded as having few moisture saving adaptations these animals frequent damp but not wet habitats under litter, bark and under rotting logs on the forest floor. Most taxa have low vagility and high endemicity. Terrestrial flatworms are generally not amenable to trapping, and are collected by handpicking. By the turn of the century some 90 Australian species and subspecies were described, presently accommodated in 12 genera within two principal families (Winsor, 1991a). On the basis of present investigations it is estimated that the total fauna is in excess of 400 species.

Taxonomy of the Terricola is based upon characters derived from the external morphology and internal microanatomy and histology of sexually mature specimens. The alpha taxonomy of the Australian Terricola is in a state of flux as the internal anatomy of many species has yet to be determined.

Whilst the Terricolan faunas of New South Wales, Victoria and Tasmania are relatively well documented, those of the remaining states are known only superficially. In Queensland only nine species of native terrestrial flatworms, all from sites below the Tropic of Capricorn, were

reported prior to this study. Terricola from this state are poorly represented in museum collections. Apart from the types of six species there are less than 20 specimen lots all from south-eastern Queensland held in museum collections. This study is part of an on-going taxonomic investigation of the Australian Terricola. It seeks to determine the composition and distribution of the Terricolan fauna of Queensland, with particular emphasis on the wet tropics, the preliminary results of which are presented here.

Materials and methods

The study is based upon specimens opportunistically collected by handpicking throughout eastern Queensland from Iron Range south to the border ranges, with particular attention to study sites in the Wet Tropics World Heritage Area (WHA), including the Paluma, Kirrama and Millaa Millaa areas. Whilst soil-dwelling and arboreal taxa are collected, there is a general bias towards handpicking species present beneath ground cover such as litter and rotting logs. Specimens are anaesthetised in 10% ethanol then fixed extended in 4% formaldehyde : 2% calcium acetate : 0.2% cobaltous nitrate aqueous solution (Winsor, 1991b). Following fixation specimens are sorted into recognisable taxonomic units (RTUs) and sexual examples

selected for anatomical study. Material for histological examination is processed to paraffin wax, serially sectioned transversely and sagittally at 8 μ m, and stained using Heidenhain's AZAN technique (Gabe, 1976).

Results and discussion

Queensland has a rich, highly diverse terricolan fauna. As a result of this study, the number of taxa known from the state has been increased over six-fold to some 62 species (Table 1). Six genera and 80% of the species are new, and will be described elsewhere. A preliminary checklist of terrestrial flatworms from Queensland is provided in Table 2.

In north Queensland (above 20°S) there is high species diversity of both rhynchodemids (nine genera) and geoplanids (seven genera). The southern region of the state (below 20°S) both

rhynchodemid (two genera) and geoplanid (six genera) diversity is less, and geoplanid taxa dominate. In the Wet Tropics World Heritage Area (Tables 2 and 3) the Rhynchodeminae have their highest generic diversity in the sclerophyll forest with five genera and six species. Four genera including *Cotyloplana* and nine species are found in rainforest. A slightly different picture emerges for the Caenoplaninae with higher generic diversity in the rainforest. Here six genera and ten species are present in rainforest, with only four genera containing five species occurring in sclerophyll forest.

The only widespread morphospecies is a *Caenoplana* sp. which occurs in tall open forest and rainforest from Iron Range south to over the southern Queensland border. Histological and other analyses of this *Caenoplana* may reveal a species complex. The majority of taxa in northern Queensland appear to be highly restricted or endemic in distribution.

The rhynchodemid genera *Digonopyla*, *Dolichoplana*, and *Cotyloplana* have not previously been recorded from the Australian mainland. Two *Cotyloplana* species are now reported from the wet tropics. *Cotyloplana* species have previously been described from Lord Howe Island, and others from Indonesia. Eleven species of *Dolichoplana* are presently recognised worldwide. The genus exhibits its greatest diversity in north Queensland where at least nine undescribed species have been found. *Digonopyla* is poorly known. Two species are reported from Wallacea and an undescribed species has now been found at Iron Range on Cape York. Of particular interest is an arboreal rhynchodemid. A single translucent green specimen was found on a native rainforest grape vine (Vitaceae) in the Eungella area. Arboreal flatworms are rare, and only two species from bromeliads in Costa Rica have previously been reported (Beauchamp, 1912).

Southern Queensland represents the northern limit of the range of *Parakontikia* and *Fletchamia*. The geoplanid *Artioposthia regina* exhibits a disjunct distribution pattern. Originally found at Gympie, it has now been recorded from the Windsor Tablelands in far north Queensland.

There has been an increase in the number of introduced Terricola found in the state (Table 2). The cosmopolitan flatworm *Bipalium kewense* was reported from Gympie in 1892. Since then it has become common in urban areas of Brisbane, Townsville and country areas (Winsor, 1983, 1985). Other introduced species

Table 1. Summary of families, genera, and species of terrestrial flatworms in Queensland. The numbers of a particular taxon described prior to this study are given in parentheses, with totals indicated in bold.

Rhynchodemidae	34 (2)
Rhynchodeminae	
<i>Cotyloplana</i>	2
<i>Digonopyla</i>	1
<i>Dolichoplana</i>	9
<i>Dolichoplana</i> ?	1
<i>Platydemus</i>	6
<i>Rhynchodemus</i>	3 (2)
rhynchodemids	8
new genera-new species	3
Microplaninae ?	
new genus	1
Geoplanidae	27 (7)
Caenoplaninae	
<i>Artioposthia</i>	1 (1)
<i>Australopacifica</i>	2 (2)
<i>Australoplana</i>	3 (1)
<i>Caenoplana</i>	8 (2)
<i>Fletchamia</i>	1 (1)
<i>Kontikia</i>	2
<i>Parakontikia</i>	3
geoplanid	1
new genera-new species	5
Pelmatoplaninae	
<i>Pelmatoplana</i> ?	1
Bipaliidae	1 (1)
<i>Bipalium</i>	1
Total number of species	62 (10)

Table 2. A checklist of terrestrial flatworms from Queensland. Taxa present in Wet Tropics World Heritage Area are indicated with an asterisk, and introduced species with a cross.

Rhynchodemidae	Geoplanidae
Rhynchodeminae	Caenoplaninae
<i>Cotyloplana</i> sp. 1 Millaa Millaa S/Lake	
Eacham*	<i>Artioposthia regina</i> (Dendy, 1892b)
<i>Cotyloplana</i> sp. 2 Millaa Millaa S*	
<i>Digonopyla</i> sp. Iron Range	<i>Australopacifica pava</i> (Steel, 1897)
<i>Dolichoplana</i> sp. 1 Kirrama*	<i>Australopacifica scaphoidea</i> (Steel, 1900)
<i>Dolichoplana</i> sp. 2 Townsville/Charters Towers†	<i>Australopacifica minor</i> Dendy, 1892b
<i>Dolichoplana</i> sp. 3 Iron Range	<i>Australopacifica</i> sp. Border Ranges
<i>Dolichoplana</i> sp. 4 Atherton Tablelands*	<i>Australopacifica</i> sp. Eungella
<i>Dolichoplana</i> sp. 5 Paluma*	<i>Caenoplana coerulea coerulea</i> Moseley, 1877
<i>Dolichoplana</i> sp. 6 Eungella	<i>Caenoplana bicolor</i> (Graff, 1899)
<i>Dolichoplana</i> sp. 6 Bowen	<i>Caenoplana</i> sp. 1 (widespread)*
<i>Dolichoplana</i> sp. 7 Millaa Millaa S*	<i>Caenoplana</i> sp. 2 Atherton Tablelands*
<i>Dolichoplana</i> sp. 8 Cooroy, Gin Gin	<i>Caenoplana</i> sp. 3 Eungella
<i>Dolichoplana</i> sp. 9 Paluma*	<i>Caenoplana</i> sp. 4 Magnetic Island†
? <i>Dolichoplana</i> sp. Mt Finnigan*	<i>Caenoplana</i> sp. 5 Paluma*
<i>Platydemus manokwari</i> Beauchamp, 1962†	<i>Caenoplana</i> sp. 6 Lake Barrine*
<i>Platydemus</i> sp. 1 Malanda*	<i>Fletchamia quinquelineata accentuata</i> (Steel, 1897)
<i>Platydemus</i> sp. 2 Millaa Millaa S (neck band)*	<i>Kontikia circularis</i> (Fyfe, 1956)†
<i>Platydemus</i> sp. 3 Millaa Millaa*	<i>Kontikia orana</i> Froehlich, 1955†
<i>Platydemus</i> sp. 4 Millaa Millaa (white blotched)*	<i>Parakontikia atrata</i> (Steel, 1897)
<i>Platydemus</i> sp. 5 Paluma*	<i>Parakontikia ventrolineata</i> (Dendy, 1892a)
<i>Rhynchodemus obscurus</i> Fletcher & Hamilton, 1888	<i>Parakontikia</i> sp. Miriam Vale
<i>Rhynchodemus putzei</i> Graff, 1899	geoplanid sp. Paluma (maculate)*
<i>Rhynchodemus</i> sp. Eungella (arboreal)	gen. nov. 1 sp. nov. Paluma*
rhynchodemid sp. 1 Lake Eacham*	gen. nov. 2 sp. nov. Lake Barrine*
rhynchodemid sp. 2 Kirrama (pink)*	gen. nov. 3 sp. nov. Millaa Millaa S*
rhynchodemid sp. 3 Windsor Tablelands*	gen. nov. 4 sp. nov. 1 Paluma*
rhynchodemid sp. 4 Condon	gen. nov. 4 sp. nov. 2 Russell River*
rhynchodemid sp. 5 Eprapah	Pelmatoplaninae
rhynchodemid sp. 6 Mt Stuart	<i>Pelmatoplana</i> sp. Roberston†
rhynchodemid sp. 7 Charters Towers	Bipaliidae
rhynchodemid sp. 8 Cooroy	<i>Bipalium kewense</i> Moseley, 1878†
gen. nov. A sp. nov. Charters Towers	
gen. nov. B sp. nov. Paluma*	
gen. nov. D sp. nov. Red Falls	
Microplaninae ?	
gen. nov. C sp. nov. Paluma*	

Table 3. Terricola genera of the Wet Tropics World Heritage Area. Number of species present in sclerophyll forest and rainforest.

Taxon	sclerophyll rainforest forest	
Rhynchodeminae		
<i>Cotyloplana</i>		2
<i>Dolichoplana</i>	5	1
<i>Platydemus</i>	2	2
rhynchodeminiid spp.	1	2
new genus B	1	
new genus C	1	
Caenoplaninae		
<i>Artioposthia</i>	1	1
<i>Caenoplana</i>	2	3
new genus 1	1	1
new genus 2		1
new genus 3		1
new genus 4	1	2
Totals	15	16

in northern Queensland include *Kontikia orana* (Winsor, 1986), *Platydemus manokwari*, used elsewhere for the control of the Giant African snail *Achatina fulica*, and a *Caenoplana* species. The latter two species are probably introduced from Papua-New Guinea.

Compared to many other groups of terrestrial invertebrates, terrestrial flatworms are under-represented in museum collections. In part this is possibly because they are extremely delicate, moisture and heat sensitive. Unless special precautions such as cooling are taken during collection and transport, the flatworms die and rapidly decompose. Recommended fixatives such as ethanol and simple formalin solutions (Steel, 1897, 1900) have failed to preserve the colour and pattern; most museum specimens are a featureless brown colour. For taxonomic purposes flatworms require careful anaesthesia, and good histological fixation which also maintains external morphology, colour and pattern (Winsor, 1991b).

Table 4. Occurrence of genera in south eastern Australia, southern Queensland, in north and far north Queensland above 20 degrees latitude, and in Papua New Guinea, Irian Jaya and Indonesia.

Family/Genus	SE Aust	S Qld	N Qld	FN Qld	PNG-IJ Indonesia
Geoplanidae					
<i>Artioposthia</i>	+	+	+	+	
<i>Australoplana</i>	+	+	+	+	
<i>Caenoplana</i>	+	+	+	+	
<i>Australopacifica</i>	+	+			+
<i>Parakontikia</i>	+	+			
<i>Fletcheria</i>	+	+			
new genus 1			+	+	
new genus 2			+	+	
new genus 3			+	+	
new genus 4			+	+	
Rhynchodemidae					
<i>Rhynchodemus</i>	+	+	+	+	+
<i>Platydemus</i>	+	?	+	+	+
<i>Dolichoplana</i>		+	+	+	+
<i>Cotyloplana</i>				+	+
<i>Digonopyla</i>				+	+
new genus A			+		
new genus B			+		
new genus C			+		
new genus D			+		
Totals	6	14	12	6	

Taxonomy and systematics of the Terricola are based principally upon microanatomical characters revealed by histological investigations. Biogeographical and phylogenetic analyses of the Queensland taxa are presently precluded at this early stage of investigations because of incomplete data. Terrestrial flatworms do not appear to be as numerically abundant in Queensland as they are in the south-eastern states, though this observation has not been substantiated by quantitative studies. Despite these limitations, two broad elements can be clearly recognised in the Queensland terrestrial flatworm fauna (Table 4). A southern group which is comprised largely of caenoplaninid genera dominant in southern Queensland which includes taxa present in south-eastern Australia. The other element is the northern group composed chiefly of rhynchodemid genera including taxa present in Indonesia, Irian Jaya and Papua-New Guinea. The affinities of the new caenoplaninid genera in this group have not yet been determined.

Conservation threats to terrestrial flatworms include loss of habitat through deforestation and high-frequency fuel reduction burning. Destruction of rotting logs and habitat in rainforest by feral pigs may also be significant in certain areas of the Wet Tropics WHA. Throughout Australia, small pockets of remnant forest along roadsides and on farms are often significant cryptofaunal refugia, vital for reconstructing the historic biogeography of the Terricola, and for the conservation of flatworms. Clearing and burning fallen timber on agricultural land, and the removal of fallen timber by the public for firewood are significant threats to the conservation of cryptofauna. Maintenance and augmentation of these important areas should be encouraged and included in all regional rural conservation education and management schemes.

Acknowledgments

Grants from the CSIRO Science and Industry Endowment Fund for equipment, and support from the Australian Biological Resources Study for taxonomic revisionary studies on Australian rhynchodemid terrestrial flatworms are gratefully acknowledged. Colleagues, and especially my family, are particularly thanked for their encouragement of this research and for assisting with collecting over the years.

References

- Beauchamp, P. de., 1912. Planaires terrestres des Broméliacées de Costa-Rica recueillis par M.C. Picado. *Archives de Zoologie expérimentale et générale* 50: 1–10.
- Gabe, M., 1976. *Histological techniques*. Masson: Paris.
- Steel, T., 1897. Australian land planarians: descriptions of new species and notes on collecting and preserving. *Proceedings of the Linnean Society of New South Wales* 22: 104–119.
- Steel, T., 1900. Australian land planarians. descriptions of new species and notes on collecting and preserving. No.2. *Proceedings of the Linnean Society of New South Wales* 25: 563–580.
- Winsor, L., 1983. A revision of the cosmopolitan land planarian *Bipalium kewense* Moseley, 1878 (Turbellaria: Tricladida: Terricola). *Zoological Journal of the Linnean Society* 79: 61–100.
- Winsor, L., 1985 Land planarians (Turbellaria; Tricladida: Terricola) introduced into Australia — 1. *Bipalium kewense* Moseley, 1877. *Victorian Naturalist* 103: 102 — 105.
- Winsor, L., 1986. Land planarians (Turbellaria: Tricladida: Terricola) introduced into Australia — 2. *Kontikia orana* Froehlich, 1955. *Victorian Naturalist* 103: 9–11.
- Winsor, L., 1991a. A provisional classification of Australian terrestrial geoplanid flatworms (Tricladida: Terricola: Geoplanidae). *Victorian Naturalist* 108: 42–49.
- Winsor, L., 1991b. Methods for taxonomic and distributional studies of terrestrial flatworms (Tricladida: Terricola). In: S. Tyler (ed), *Turbellarian biology*. *Hydrobiologia* 227: 349–352.

WHY ARE AMPHIBIAN HELMINTH COMMUNITIES DEPAUPERATE?

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Abstract

Barton, D.P., 1997. Why are amphibian helminth communities depauperate? *Memoirs of the Museum of Victoria* 56(2): 581–586.

The helminth community structure of the introduced toad, *Bufo marinus*, and the native frog, *Litoria inermis*, are compared, for the first time. Previous studies have found the helminth communities of amphibians to be depauperate although no study has previously detailed a community from a tropical host species. Both *B. marinus* and *L. inermis* were infected with a higher number of helminth species than the previously recorded anuran average, but contained fewer individuals. The use of the core and satellite species concept in these depauperate communities is considered incorrect due to the isolationist characteristic of the communities.

Introduction

The community ecology of helminths is emerging as an informative field of research, although amphibians have received little attention from parasite ecologists (Lluch et al., 1987; Aho, 1990; Esch et al., 1990). The majority of work on helminths of these hosts has concentrated on faunistic surveys or discussions on phylogenetic relationships between host and parasite (see Aho, 1990; Muzzall, 1991b). Studies of the helminth fauna of amphibians at the infracommunity level are, however, practically non-existent (Aho, 1990), despite the fact that this level of study comprises the basic data collected in any parasitological survey (Holmes and Price, 1986).

The helminth communities of amphibians have been found by various workers to be depauperate (low in species richness) and isolationist in character. Examples of this type of community have been reported for salamanders (Goater et al., 1987; Aho, 1990; Muzzall, 1990, 1991a) and frogs (Muzzall, 1991b). However, comparatively rich helminth faunas have been reported from ranid frogs in Poland (Kuc and Sulgostowska, 1988a, 1988b). From his review of amphibian parasite literature, Aho (1990) found that anurans had an average richness of 0.98 helminth species per host individual, while salamanders were slightly lower with an average of 0.7.

The community ecology of helminths within amphibians in Australia has never been documented especially for the introduced toad, *Bufo marinus*. This paper aims to describe the dynamics of the helminth communities within

the introduced toad compared to a native amphibian, *Litoria inermis*.

Materials and methods

Bufo marinus and *Litoria inermis* were collected from 'Bentley', a privately owned property at the 'Bentley Estate', approximately 30 km south of Townsville in April 1991. Animals were kept overnight and dissected the following day; dissection followed a fatal dose (2–5 drops, dependent on size) of 'Lethabarb' (Euthanasia injection Pentobarbitone solution) sprinkled onto the dorsal surface. A ventral incision was made from the pelvic to the pectoral girdle exposing the body cavity. The following organs were removed and placed in separate dishes containing a 0.8% sodium chloride solution for inspection: lungs, stomach, intestine and rectum, urinary bladder, kidney, liver and gall bladder. Occasionally, the mouth cavity, nostrils, heart, and leg musculature were also examined. Organs were examined under a stereo microscope using transmitted light.

Helminths were removed from dissected organs with the aid of fine dissecting forceps; numbers and location within host for each type of helminth were recorded.

Definitions of ecological terms follow Margolis et al. (1982). Prevalence of infection is the percentage of hosts infected in a sample. Mean intensity of infection is the average number of helminth individuals per infected host. Total helminth intensity is the total number of helminth individuals of all helminth species per host individual. Species richness is the number of helminth species per host.

Analyses of helminth community structure were carried out at the infracommunity (host individual) and component community (host species) level. Measures of infracommunity structure used were: mean number of helminth individuals per host individual, mean number of helminth species per host, and mean Brillouin's index per host (infected hosts only). Measures of component community structure (taken from grouped data) were: total number of helminth species, number of component species, Simpson's index, and Shannon-Weiner index. Analyses of community structure follow methods as outlined by Magurran (1988). Values for indices were calculated for each infracommunity and included all helminths, irrespective of site of infection, using natural logarithms (\log_e). The final statistic is expressed as a mean (\bar{x}) \pm SE \bar{x} .

Analysis of the similarity of the helminth communities of *B. marinus* and *L. inermis* was completed with a Jaccard similarity index following the methods outlined by Magurran (1988). Comparison of the helminth community structure between *B. marinus* and *L. inermis* was done by a two sample t-test.

Helminth species are determined as core species if their prevalence of infection is over 70%, secondary species if 40–70%, or satellite species if less than 40% (Stock and Holmes, 1987). A component species is defined as having a prevalence of at least 10% (Bush et al., 1990).

Results

A total of 33 *B. marinus* and 53 *L. inermis* were collected from Bentley in April 1991. Twelve helminth species were collected from *B. marinus* and *L. inermis*: 5 digeneans (*Mesocoelium* sp., *Dolichosaccus symmetrus*, *D. juvenilis*, *D. helocirrus*, *Pleurogenoides* sp.), 5 nematodes (*Rhabdias* sp., *Maxvachonia* sp., *Johnpearsonia pearsoni*, *Cosmocerca* sp.1, Nematode larvae) and 2 cestodes (*Nematotaenia hylae*, *Diphyllobothrium* sp. larvae) (Table 1). *Bufo marinus* was infected with 9 helminth species and *L. inermis* with 8 species; 5 of these helminth species were shared (see Table 1). The Jaccard similarity index of the helminth communities of *B. marinus* and *L. inermis* was 0.417. *Rhabdias* sp. was the most commonly encountered helminth for both host species.

Of the 33 toads collected, 28 (84.8%) were infected with at least one helminth; 47 (88.7%) of 53 *L. inermis* were infected with at least one helminth (Figure 1). Table 2 presents general

infection parameters for both *B. marinus* and *L. inermis* compared to values calculated by Aho (1990) for anurans. Both *B. marinus* and *L. inermis* were infected with more helminth species than has been recorded as the anuran average; intensity of infection was below the anuran average.

The diversity characteristics of the infracommunities of *B. marinus* and *L. inermis* are presented in Table 3. *Bufo marinus* was infected with a significantly higher mean number of helminths ($t_{31}=2.57$, $p=0.015$), mean number of helminth species ($t_{44.8}=2.65$, $p=0.011$) and mean Brillouin's index ($t_{39.9}=3.01$, $p=0.005$).

The diversity characteristics of the component communities of *B. marinus* and *L. inermis* are presented in Table 4. Only 4 helminth species for *B. marinus*, and 2 for *L. inermis*, were considered component species (prevalence >10%; see Table 1). *Rhabdias* sp. was the only component species infecting both host species. *Bufo marinus* had higher values for the Simpson's Index and the Shannon-Weiner Index.

Discussion

The helminth communities of *B. marinus* and *L. inermis* have been documented for the first time. Despite the limited geographical and seasonal nature of the study, some important data are revealed.

In general, the characteristics of the helminth fauna of *B. marinus* and *L. inermis* correspond to those outlined by Aho (1990) for anurans. The helminth community is depauperate and isolationist in character. The community is considered isolationist due to the low number of helminth species and individuals present (see Sousa, 1994).

Average species richness for both *B. marinus* and *L. inermis* was higher than the average of 0.98 calculated by Aho (1990) for anurans in general (see Table 2). Average helminth intensity for both species, however, was below the anuran average. The studies reviewed by Aho (1990) were primarily based in temperate climates (North America and Europe) and the results found in this study may be due to its tropical location. This relationship, however, requires further work detailing the communities within various tropical amphibian species to determine its accuracy.

Bufo marinus was found to have a significantly more diverse helminth community than *L. inermis*. Higher values for all parameters were

Table 1. Helminth infracommunities of 33 *Bufo marinus* and 53 *Litoria inermis* collected from Bentley in April 1991.

Helminth Species	Site	<i>Bufo marinus</i>				<i>Litoria inermis</i>			
		No. Infected (%)	Mean Intensity	SE \bar{x}	Maximum Infection	No. Infected (%)	Mean Intensity	SE \bar{x}	Maximum Infection
<i>Mesococclium</i> sp.	Intestine	9 (27.3)	5.1	1.3	12	2 (3.8)	1.0	0.0	1
<i>Dolichosaccus symmetricus</i>	Intestine	1 (3.0)	2.0	0.0	2	1 (3.0)	1.0	0.0	1
<i>Dolichosaccus juvenilis</i>	Intestine	1 (3.0)	10.0	0.0	10				
<i>Dolichosaccus helocirrus</i>	Intestine	4 (12.1)	4.5	1.2	8				
<i>Pleurogenoides</i> sp.	Intestine	3 (9.1)	6.3	2.3	10	4 (7.5)	8.5	4.7	22
<i>Rhabdias</i> sp.	Lung	25 (75.8)	6.3	2.1	49	44 (83.0)	2.0	0.3	10
<i>Maxvachonia</i> sp.	Intestine	6 (18.2)	2.5	1.1	8	1 (1.9)	2.0	0.0	2
<i>Johnpearsonia pearsoni</i>	Intestine	3 (9.1)	1.0	0.0	1				
<i>Cosmocerca</i> sp. 1	Rectum	1 (3.0)	1.0	0.0	1				
Nematode larvae	Mesenteries					1 (1.9)	1.0	0.0	1
<i>Nematotaenia hylae</i>	Intestine					1 (1.9)	1.0	0.0	1
<i>Diphyllobothrium</i> sp. (larva)	Leg muscles					6 (11.3)	3.3	0.8	7

Table 2. Helminth intensity and species richness within communities from *Bufo marinus* and *Litoria inermis* compared to values for anurans as calculated by Aho (1990).

		Helminth Intensity	Species Richness
<i>Bufo marinus</i> (This study)	Mean Intensity (SE \bar{x})	8.18 (2.12)	1.57 (0.19)
	Range of Infection	0–52	0–5
<i>Litoria inermis</i> (This study)	Mean Intensity (SE \bar{x})	2.89 (0.59)	1.15 (0.11)
	Range of Infection	0–25	0–4
Anurans (Aho, 1990)	Mean Intensity (SE \bar{x})	11.55 (1.86)	0.98 (0.07)
	Range of Infection	0–45	0–9

Table 3. Diversity characteristics of the infracommunities of helminths of *Bufo marinus* and *Litoria inermis* (infected hosts only) collected from Bentley in April 1991.

Characteristic	<i>Bufo marinus</i>	<i>Litoria inermis</i>
Number of infected hosts	28	47
Mean number of helminth individuals (SE \bar{x})	9.64 (2.40)	3.26 (0.65)
Mean number of helminth species (SE \bar{x})	1.86 (0.18)	1.30 (0.11)
Mean Brillouin's index (SE \bar{x})	0.30 (0.06)	0.09 (0.03)
Mean evenness (SE \bar{x})	0.48 (0.09)	0.16 (0.05)

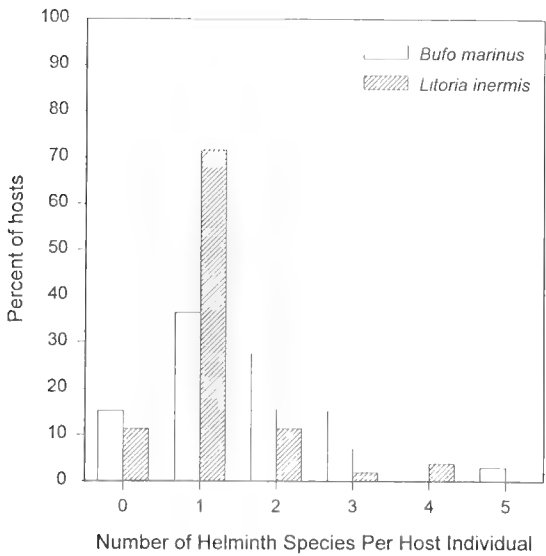


Figure 1. Distribution of number of helminth species per host individual for *Bufo marinus* and *Litoria inermis* collected from Bentley.

Table 4. Diversity characteristics of the component communities of helminths of infected *Bufo marinus* and *Litoria inermis* collected from Bentley in April 1991.

Characteristic	<i>Bufo marinus</i>	<i>Litoria inermis</i>
Number of helminth species	9	8
Number of component species	4	2
Simpson's index	2.65	2.50
Shannon-Weiner index	1.37	0.98

recorded for *B. marinus* at both the infracommunity and component community levels. Although helminth species were shared between the host species, level of similarity was below 0.5. In addition, infection levels were generally higher in *B. marinus*. These results are of interest considering that *B. marinus* is an introduced

host to Australia that has acquired the majority of its helminths from Australian native frogs and reptiles (Barton, 1995). The toad, therefore, would appear to have successfully adapted to the Australian parasite fauna, and them to it. The helminths of these native hosts, therefore, would appear not to be highly host-specific.

Possible reasons for *B. marinus* having the more diverse helminth community include host size, diet, habit and habitat differences.

The average host size of *L. inermis* is considerably smaller than that of *B. marinus* (pers. obs.). Further studies of native amphibians of sizes closer to the toad (for example, *Cyclorana* species) need to be undertaken to determine the true extent of the relationship of host size to helminth community dynamics.

Bufo marinus is a wide foraging predator (Strüssmann et al., 1984) whereas *L. inermis* is an ambush predator (pers. obs.). The diet of the two host species at Bentley differed in the size (small for *L. inermis* and large for *B. marinus*) and the variety (small flying insects for *L. inermis* and large beetles, ants, large flying insects for *B. marinus*) of prey taken. Ambush predators, theoretically, have a less diverse helminth fauna due to the lower variety of prey encountered (Aho, 1990). Of the eight helminth species collected from *L. inermis* in April 1991, six are reliant on dietary transmission (see Prudhoe and Bray, 1982). The helminth fauna of *B. marinus*, however, has only five of the nine species reliant on dietary transmission.

The majority of the nematodes in this study have direct life cycles (see Anderson, 1992) either through skin penetration (for example *Rhabdias* sp.) or consumption of infective larvae. Kennedy et al. (1986) and Aho (1990) suggested that nematodes with direct life cycles would play a major role in the species richness of isolationist helminth communities, as were found here.

The concept of core and satellite parasite species was proposed by Hanski (1982) and has since been adapted to parasite communities. Core species are generally single host species specialists, adapted to each other and widespread and abundant within that host species. Satellite species are acquired by exchange from the ecological associates of the host and are sporadic and less abundant. Within an intra-community, it is the core species that will interact, usually in a negative association, whereas secondary species are isolated from other species (Sousa, 1994). In exchange, one host's core species becomes another's satellite species

(Freeland, 1983; Holmes and Price, 1986). Aho (1990) suggested, however, that due to the isolationist characteristic of amphibian parasite communities, that species be considered either common (prevalence over 50%) or rare (below 50%).

The concept of core and satellite species works well in highly diverse and species rich helminth communities, such as those found in aquatic birds (see Stock and Holmes, 1987). In species-poor communities, such as those found in amphibians, however, such terms are inadequate. Helminth communities of amphibians are generally made up of host generalists which freely exchange between host species. This makes the community, by definition (see Bush and Holmes, 1986), satellite. For such species-poor communities even the classification of species as common or rare (see Aho, 1990) does not detail the community sufficiently. Listing the component species (prevalence greater than 10%; Bush et al., 1990) would give a better idea of the diversity of the community.

The study of the community ecology of helminths of amphibians is an informative field. This field is in its infancy, however, and requires more work to be carried out on communities within tropical amphibians. It is hoped that this study will provide the starting step for future ecological studies of amphibian species in Australia.

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References

- Aho, J.M., 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. Pp. 157–195 in: Esch, G.W., Bush, A.O. and Aho, J.M. (eds), *Parasite communities: patterns and processes*. Chapman and Hall: London.
- Anderson, R.C., 1992. *Nematode parasites of vertebrates: their development and transmission*. C.A.B.: Oxon.
- Barton, D.P., 1995. *The cane toad: a new host for helminth parasites in Australia*. PhD Thesis, James Cook University of North Queensland, Australia.

- Bush, A.O. and Holmes, J.C., 1986. Intestinal helminths of lesser scaup ducks: patterns of association. *Canadian Journal of Zoology* 64: 132–141.
- Bush, A.O., Aho, J.M. and Kennedy, C.R., 1990. Ecological versus phylogenetic determinants of helminth parasite community. *Evolutionary Ecology* 4: 1–20.
- Esch, G.W., Shostak, A.W., Marcogliese, D.J. and Goater, T.M., 1990. Patterns and processes in helminth parasite communities: An overview. Pp. 1–19 in: Esch, G.W., Bush, A.O. and Aho, J.M. (eds), *Parasite communities: patterns and processes*. Chapman and Hall: London.
- Freeland, W.J., 1983. Parasites and the coexistence of animal host species. *American Naturalist* 121: 223–236.
- Goater, T.M., Esch, G.W. and Bush, A.O., 1987. Helminth parasites of sympatric salamanders: ecological concepts at infracommunity, component and compound community levels. *American Midland Naturalist* 118: 289–300.
- Hanski, I., 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210–221.
- Holmes, J.C. and Price, P.W., 1986. Communities of parasites. Pp. 187–213 in: Anderson, D.J. and Kikkawa, J. (eds), *Community ecology: pattern and process*. Blackwell Scientific Publications: Oxford.
- Kennedy, C.R., Laffoley, D.d'A., Bishop, G., Jones, P. and Taylor, M., 1986. Communities of parasites of freshwater fish of Jersey, Channel Islands. *Journal of Fish Biology* 29: 215–226.
- Kuc, I. and Sulgostowska, T., 1988a. Helminth fauna of *Rana ridibunda* Pallas, 1771 from Goclawski Canal in Warszawa (Poland). *Acta Parasitologica Polonica* 33: 101–105.
- Kuc, I. and Sulgostowska, T., 1988b. Helminth fauna of frogs in the forest of Kampinos near Warszawa. *Acta Parasitologica Polonica* 33: 267–272.
- Lluch, J., Roca, V., Navarro, P. and Mas-Coma, S., 1987. Helminthofauna de los herpetos ibéricos: estado actual de conocimientos, consideraciones ecológicas y estimaciones corológicas. Pp. 143–161 in: Sans-Coma, V., Mas-Coma, S. and Gosalbez, J. (eds), *Mamíferos y Helminthos*. Barcelona.
- Magurran, A.E., 1988. *Ecological diversity and its measurement*. Croom Helm Limited: London.
- Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M. and Schad, G.A., 1982. The use of ecological terms in parasitology (Report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology* 68: 131–133.
- Muzzall, P.M., 1990. Endoparasites of the red-backed salamander, *Plethodon c. cinereus*, from southwestern Michigan. *Journal of the Helminthological Society of Washington* 57: 165–167.
- Muzzall, P.M., 1991a. Helminth infracommunities of the newt, *Notophthalmus viridescens*, from Turkey Marsh, Michigan. *Journal of Parasitology* 77: 87–91.
- Muzzall, P.M., 1991b. Helminth infracommunities of the frogs *Rana catesbeiana* and *Rana clamitans* from Turkey Marsh, Michigan. *Journal of Parasitology* 77: 366–371.
- Prudhoe, S. and Bray, R.A., 1982. *Platyhelminth parasites of the Amphibia*. British Museum (Natural History) and Oxford University Press: Oxford.
- Sousa, W.P., 1994. Patterns and processes in communities of helminth parasites. *Trends in Ecology and Evolution* 9: 52–57.
- Stock, T.M. and Holmes, J.C., 1987. Host specificity and exchange of intestinal helminths among four species of grebes (Podicipedidae). *Canadian Journal of Zoology* 65: 669–676.
- Strüssmann, C., Riberio do Vale, M.B., Meneghini, M.H. and Magnusson, W.E., 1984. Diet and foraging mode of *Bufo marinus* and *Leptodactylus ocellatus*. *Journal of Herpetology* 18: 138–146.

AN *EX SITU* BREEDING PROGRAMME FOR THE ENDANGERED UK POPULATION OF THE FIELD CRICKET *GRYLLUS CAMPESTRIS*

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Abstract

Pearce-Kelly, P., Croft, P., Atkin, P. and Clarke, D., 1997. An *ex situ* breeding programme for the endangered UK population of the field cricket *Gryllus campestris*. *Memoirs of the Museum of Victoria* 56(2): 587-589.

In 1991 the British population of the field cricket *Gryllus campestris* was close to extinction with fewer than a hundred individuals remaining in the single surviving colony. A key component of English Nature's recovery programme for the species involved the creation of six new colonies in areas of the cricket's former UK range. This objective required the establishment of a captive-breeding programme to provide the large number of animals needed to found the new colonies. Between 1992 and 1995 >4000 captive-bred nymphs were released into five new sites. Monitoring confirmed that the release populations are becoming successfully established.

Introduction

By virtue of their small size, modest accommodation requirements and often substantial reproductive potential, many invertebrate species can be maintained as large captive populations retaining levels of genetic variation necessary to achieve successful field re-introduction and establishment (Morton, 1991; Pearce-Kelly, 1994). Experience has also shown that invertebrate conservation programmes can hold their own when it comes to generating public interest and support. These considerations make many invertebrate species excellent candidates for receiving captive-breeding assistance as part of conservation programme work. An example of the efficacy of providing captive breeding assistance to an endangered invertebrate species is the conservation programme for the UK population of the field cricket, *Gryllus campestris* L., 1758.

Although a relatively common species on the European continent, by 1991 the British population of *G. campestris* had been reduced to a single surviving colony in West Sussex, numbering fewer than 100 individuals and is recorded as Endangered in the British Red Data Book (Shirt, 1987). The reason for the species decline in the UK was essentially loss of its close growing turf sites, which need to be situated on porous sandy soil and to have a sheltered and sunny aspect. A prime cause of this habitat loss has been overgrowth of vegetation, as a result of changes in grazing practices. In an effort to safeguard the surviving UK population and expand the number of colonies, the conservation body English

Nature has placed the field cricket onto its Species Recovery Programme. This conservation initiative is directed at recreating the cricket's habitat requirements over areas of its former range and identifying existing alternative sites that already provide suitable habitat.

In autumn 1991 English Nature (EN) and the Zoological Society of London (ZSL) agreed on a protocol to establish a captive-breeding programme, based at the London Zoo's Invertebrate Conservation Centre, to support EN's ongoing Species Recovery Programme for the field-cricket. The protocol involved using wild caught crickets from the sole surviving mainland colony to provide a founder breeding stock to produce the large numbers of captive bred crickets required to populate new colony sites. In the late spring of 1992, six pairs of sub-adult field crickets were collected from the remaining wild colony in West Sussex (Edwards, 1992) and taken to the Zoo's Invertebrate Conservation Centre.

Captive-breeding and rearing conditions

Upon arrival at the Zoo the sub-adult crickets were initially kept separate in plastic tanks 18 x 33 x 18 cm high. The substrate consisted of sterilised Imms No.2 potting soil to a depth of 12cm. Each tank was provided with a sod of turf (collected from the original colony site) to encourage the crickets to excavate a burrow, which they readily did. Drainage holes in the base of the tanks allowed for frequent watering of the substrate. Upon reaching adult the crickets were paired up in the same tanks.

Temperature and humidity levels were aimed at mimicking the recorded field conditions as faithfully as possible. In addition to maintaining a fluctuating day/night background temperature, a 60 watt light bulb was suspended over each of the breeding and rearing tanks to provide radiant basking opportunities. The bulbs were on from 09.00–12.00h and from 13.00–18.00h which elevated maximum temperatures to the low 30s (°C). At night the room temperature dropped to 15°C. Mean humidity levels in the rearing tanks was approximately 50%.

Mated females oviposited directly into the soil substrate of the breeding tanks. Upon hatching, nymphs were left in the breeding tanks until the 2nd or 3rd instar when they were transferred to nymphal rearing tanks 30 × 45 × 30cm high. The rearing tanks were provided with 6 cardboard egg trays stacked at one end of each tank to maximise opportunities for successful moulting, basking and shelter. Care was taken to ensure that offspring of different females were maintained as separate progeny lines.

The overwintering requirements of the crickets were best met by exposing the nymphs to the rigours of a British winter. This was achieved by placing nymphs in unheated external insect rearing units, either in their rearing tanks or into 1.5 m-square external bays with a deep soil and turf substrate to allow more natural overwintering conditions.

The crickets were presented with a variety of vegetables, fruits, leaves and grasses with the most popular food items being fresh lettuce, apple, and carrot. Bran and cuttlebone (a calcium supplement) were also provided. Females were occasionally given the larvae of the wax moth, *Galleria mellonella* which were often accepted. The provision of fish-flakes mid way through the programme was seen as an important protein supplement for nymphs and adults. Free water was provided in the form of damp cotton wool and regular spraying with distilled water.

Results

Crickets were paired up within a week or so of reaching adult in early summer and were observed to mate repeatedly in the breeding tanks. The first hatching were observed in mid June implying a development period of 26 days (Pearce-Kelly and Croft, 1995). The first three years (1992–1995) of the breeding programme produced > 4000 crickets for field release. These animals were used to establish five new

colony sites selected by English Nature. Prior to release the different progeny lines were amalgamated so as to ensure maximum genetic mix for colony establishment.

Regular monitoring of the introduction sites has confirmed the successful overwintering of sufficient numbers of the captive-bred crickets to ensure the production of the F1 wild generation. These F1 crickets have in turn gone on to produce the F2 wild generation (Edwards, 1995).

In addition to providing large numbers of animals for colony establishment, the captive-breeding programme is helping to clarify some important biological questions, such as sex ratios and fecundity data, that would otherwise be impossible to ascertain. By summer 1995 the results of the field cricket recovery programme were such that English Nature was able to declare the species secure in the UK.

Conclusion

The captive-breeding programme for *G. campestris* highlights how successful and cost-effective such conservation work for invertebrate species can be. By allocating even modest resources to develop captive-breeding programmes for invertebrates facilities, such as zoos can significantly increase their ability to play a major role in species conservation (Pearce-Kelly, 1994).

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References

- Edwards, M., 1992. *Species recovery programme field cricket*, *Gryllus campestris*, *Field report for 1992 to English Nature*. English Nature: Peterborough.
- Edwards, M., 1995. *Species recovery programme field cricket*, *Gryllus campestris*, *Field report for 1995 to English Nature*. English Nature: Peterborough.
- Morton, A.C., 1991. Captive breeding of butterflies and moths: 11. Conserving genetic variation and managing bio-diversity. *International Zoo Yearbook* 30: 89–97.
- Pearce-Kelly, P., 1994. Invertebrate propagation and re-establishment programmes: the conservation and education potential for zoos and related institutions. Pp. 329–337 in: Olney, P.J.S., Mace, G.M. and Feistner, A.T.C. (eds), *Creative conser-*

- vation: *interactive management of wild and captive animals*. Chapman and Hall: London.
- Pearce-Kelly, P. and Croft, P., 1995. *Progress report on the ZSL captive-breeding programme for the field cricket Gryllus campestris*. Zoological Society of London: London.
- Shirt, D.B., 1987. *British Red Data Book: 2. Insects*. Nature Conservancy Council.

CONSERVATION OF CAVE FAUNA: MORE THAN JUST BATS

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Abstract

Slaney, D.P. and Weinstein, P., 1997. Conservation of cave fauna: more than just bats. *Memoirs of the Museum of Victoria* 56(2): 591-596.

The expansion of biospeleology as a science and caving as a recreational activity have led to a corresponding increase in pressure on caves and their ecosystems. The threats include direct human disturbance from visitation, and indirect modifications to cave habitats and the surrounding environment. Despite the high profile of conservation issues such as the threat to populations of ghost bats, little work has been carried out in Australia to assess the impact of humans on cave ecology. The aim of this study was to briefly review the effects of disturbance on populations of cave invertebrates, and to investigate the impact that sampling may have upon them.

We recorded the weekly total of individuals of each macroinvertebrate species collected over one month of continuous trapping with a variety of methods in Rope Ladder Cave, Fanning River Caves, North Queensland. The results indicated that numbers of pseudoscorpions, cockroaches, rhizophagid beetles, and pselaphid beetles declined significantly over the sampling period. Sampling of cave invertebrates for scientific purposes may therefore have an impact on the population dynamics of cave species, and may consequently affect the ecology of the cave itself. We recommend that the general ecology of organisms in a cave be investigated before any intensive sampling is carried out, and that where possible, sampling with replacement should be used.

Introduction

Cave environments are unique habitats that are suffering from increasing pressures placed upon them. Caves contain a wide range of invertebrate taxa, such as crickets, cockroaches, millipedes, amphipods, isopods, and arachnids. Many of these organisms show morphological modifications (troglomorphies) that are not found in corresponding surface dwelling (epigean) species. Troglomorphies include reduction or loss of eyes, wings, and bodily pigmentation, and attenuation of appendages (Barr, 1968; Culver, 1982; Kane and Richardson, 1985). Many of these species are relicts, having few or no closely related epigean species. Although a large amount of research has been carried out on Australia's temperate caves (Hamilton-Smith, 1967, 1987; Richards, 1971; Eberhard, 1993; Eberhard *et al.*, 1991), few studies have looked at our tropical caves. Not until the early 1980s did entomological studies delve deeper into North Queensland caves. This work led to the discovery of a rich and diverse range of tropical cave fauna including sandflies, plant hoppers, assassin bugs, and cockroaches (Lewis and Dyce, 1983; Hoch and Howarth, 1989a, b; Malipatil and Howarth, 1990; Roth, 1990). One expedition by Howarth and Stone in 1985 recorded over 40 species of cave arthro-

pods from Bayliss lava tube at Undara, seven of which were new species (two represent new genera) and 24 of which were troglobites (Howarth and Stone, 1990). We have discovered further new species, including a pseudoscorpion, and several sibling species of cave cockroaches (Weinstein and Slaney, 1995). Caves are not only important with respect to documenting and preserving biodiversity, but are important for studying adaptation, speciation, and species interactions. They provide us with natural laboratories in which we can frame and test evolutionary hypotheses.

Cave organisms are particularly vulnerable to disturbance as they live within discrete habitats, with isolated island like distributions. Species are particularly vulnerable when endemic species are confined to one or two caves within a karst region. For example, near Chillagoe, Qld, four small limestone towers occur within a 2 km² area within which several endemic cave adapted arthropods are found, with some being restricted to single towers (Hoch and Howarth, 1989b). Population sizes are often small, and due to their isolated distribution may exhibit a limited gene pool and restricted gene flow, which may result in severe bottle necks, further increasing their vulnerability (Barr and Holsinger, 1985; Caccone, 1985; Culver, 1986). The small size of

caves, compared to surface habitats, also reduces the resilience of such species to disturbance. Disturbances may not only result in the extinction of these organisms, but in the destruction of the unique cave habitat itself. Disturbances can be categorised as either indirect (brought about by modifications to cave habitats and the surrounding environment) or direct (brought about by human visitation to caves).

Indirect disturbance

Deforestation

Clearing of vegetation for timber, mining, and road construction changes local hydrology, and causes severe erosion and increased frequency and intensity of flooding (Lichon, 1993). In NSW and Victoria approximately 60% of the karst regions have had their native vegetation removed or severely modified (Eberhard and Spate, 1995), while in Tasmania, most caving areas are covered by intact temperate forest which is under threat by clearing for the wood-chipping industry (Lichon, 1993). Populations of glow worms in Flowery Gully caves, Tasmania, were wiped out as a result of clearing vegetation, an act which made a once permanent subterranean stream become intermittent, in turn lowering the high humidity in the caves required by the glow worms (Lichon, 1993). Clearing of vegetation near caves also removes the major source of nutrient input, dramatically lowering the food available to cave invertebrates.

The exposure of soils surrounding caves caused by clear felling, quarrying, and farming increases the rate of erosion, resulting in high levels of sediment deposition in caves (Kiernan, 1988). High levels of erosion at an Ida Bay quarry, in Tasmania, has caused clay to be washed into surrounding caves (Lichon, 1992). The deposition of clay in cave passages normally containing gravel substrates has led to the loss of cave invertebrates adapted to living in such habitats (Eberhard, 1995). Scouring of organisms from their stream habitat can also occur during periods of flooding (Chutter, 1969), while at Mole Creek Caves, Tasmania, land clearing has resulted in rapid subsidence and collapse of cave systems (Lichon, 1993).

Changing water levels

Flooding induced by land clearance or by the construction of dams can obliterate entire cave communities. Cave communities at Texas in Queensland, Burrinjuck in NSW, Dartmouth in Victoria and Lorinna in Tasmania have all been

lost as a result of dam constructions (Eberhard and Spate, 1995). Alternatively, lowering the water table can have a similar effect on cave invertebrates. In Yanchep, Western Australia, groundwater pumping is threatening aquatic cave species (Jasinska and Knott, 1991). In the Naracoorte caves, South Australia, the transpiration from overlying pine plantations has reduced the amount of water seeping into the caves, resulting in cave desiccation.

Quarrying

In addition to changing local flow regimes and increasing sedimentation rates, quarrying of limestone for cement and other building materials (eg marble) often entails the complete destruction of a cave and even entire karst tower systems. Blasting in the vicinity of caves can also cause severe structural damage to them, altering the microclimate within. Limestone operations at Mount Etna, Queensland, have led to numerous caves being destroyed, including ghost bat (*Macroderma gigas*) maternity caves (Eberhard and Spate, 1995), and presumably their associated invertebrate cave communities.

Pollution

Caves are often used for dumping of agricultural, industrial and public waste. The occurrence of sudden large influxes of nutrients (eg dead farm animals) can lead to the introduction of surface invertebrates and allow some cave species to out-compete others, upsetting the delicate ecological balance (Chapman, 1993). From 1900 to 1976 waste and wash water from a cheese factory and abattoir in Yahl, Mount Gambier, South Australia, was discharged into an unconfined limestone aquifer. The effluent contaminated groundwater, resulting in abnormally high nitrate levels in the surrounding limestone karst (Slaney and Ragusa, 1990). At Mole Creek, Tasmania, stock access to karst regions and dairy effluent runoff has increased nutrient levels, resulting in high bacterial populations in cave waters (Lichon, 1993). Pesticides and fertilisers may also be washed into caves from surrounding agricultural land (Chapman, 1993, Lichon, 1993). Cave entrances may not only be blocked by waste but infilled to make way for farming, roads and housing developments. Such blockages lead to a decrease in the amount of nutrient input into the cave ecosystem and result in the depletion or extinction of cave invertebrates (Culver, 1986).

Tourism

Construction of paths and walkways, lighting, gates on cave entrances, and widening of cave

entrances for tourism, create a number of problems for cave organisms (e.g., Webb, 1984). These constructions lead to the alteration and loss of habitat, upon which highly adapted organisms depend, by altering cave temperatures, humidities and atmospheric composition (e.g., Pugsley, 1984). Artificial lighting used for tourism can enable the establishment of plants that would not be able to survive in the normal conditions of little to no light. In turn, introduced plants may provide habitat for surface dwelling invertebrates, thus altering cave community composition (Howarth, 1982; Eberhard and Spate, 1995). Construction of gates with low sills have a tendency to trap leaf litter which would otherwise be washed into caves, as has occurred at the entrance to Kubla Khan Cave in Tasmania (Spate and Hamilton-Smith, 1991). Changes to cave microclimates also affect bat maternity sites and associated cave invertebrates (Tuttle, 1979). The placement of air tight doors to control desiccation of speleothems in Alexandra Cave at Naracoorte, South Australia, has wiped out populations of rhabdophorid cave crickets (Hamilton-Smith, 1987).

Direct disturbance

Damage to caves and the loss of cave fauna may be caused directly by human visitation. Visits by the general public, caving clubs, and researchers result in the trampling of some cave invertebrates (Spate and Hamilton-Smith, 1991), and the compaction of cave floor sediments occupied by others (e.g., crickets and beetles, Middleton, 1979). At Mount Widderin Cave, Skipton, Victoria, an invertebrate community living on unconsolidated substrate has disappeared as a result of soil compaction by high numbers of human visitors (Spate and Hamilton-Smith, 1991). In addition to soil compaction, walking through cave pools may adversely affect aquatic invertebrates. In Tasmania, rare psammaspid and syncarid crustaceans are confined to such habitats (Eberhard, 1993), and alterations of turbidity in their waters may critically alter their environment. Cave visitors also pose a potential threat to cave invertebrates by introducing organisms from the surface and from other caves which may out-compete and displace the extant cave fauna. Cave visitation may also result in the trampling of plant roots, leading to the loss of root feeding invertebrates and their predators (Howarth, 1982). Cave visitors using acetylene torches may

also impact on cave organisms through the toxic calcium carbide by-product of these torches.

Generally, caves as discrete confined habitats tend to have a carrying capacity of visitation, above which level of disturbance collapse of cave communities is likely to occur (Howarth and Stone, 1982, Spate and Hamilton-Smith, 1991). Field data on cave fauna distributions in Hawaiian lava tubes by Howarth and Stone (1982) show that species diversity and population levels are inversely proportional to the level of visitation and human disturbance. Disturbance of bat colonies brought about by human visitation, (particularly by bat researchers !) has contributed to the decline of many colonies (Tuttle, 1979). Bat decline from human disturbance has been observed in central and south-eastern NSW caves (Hall and Dunsmore, 1974). In turn, the loss of bats has led to the loss of endemic guanophilic invertebrates.

Impact of scientific studies

Despite the high profile of conservation issues such as the threat to populations of ghost bats, little work has been carried out in Australia to assess the impact of humans on cave ecology, with no studies on the effect that trapping may have on cave invertebrate populations. Key (1978) and Heath (1987) claimed that there is no evidence of collecting ever affecting a population of insects detrimentally. However, declining populations of the collected Bathurst Copper Butterfly suggest otherwise (Dexter and Kitching, 1993), and we provide evidence in this paper that intensive sampling of cave invertebrates can deplete populations. Culver (1986) stated that worldwide, one of the dangers to cave fauna is the appalling number of species threatened by over-collecting for scientific purposes, but he cites few data to support this statement. With this in mind we analysed past data we had obtained in investigations of tropical cave fauna, to assess the impact that our sampling may have had on populations of cave invertebrates.

During August 1993 we surveyed the macroinvertebrate fauna of Rope Ladder Cave, Fanning River Caves, in tropical north Qld, and recorded the weekly total of individuals of each macroinvertebrate species collected over one month of continuous trapping with four different methods concurrently (pitfall only, baited pitfall, leaf litter dry, and leaf litter wet, with no replacement; Weinstein and Slaney, 1995). Four species were trapped in sufficient numbers to look for trends in their frequency of capture.

Pseudoscorpions, cockroaches, rhizophagid beetles, and pselaphid beetles showed a significant decline in number over the sampling period (from 12, 44, 680 and 18 individuals to 5, 25, 250 and 4 individuals respectively). Given that sampling occurred at the same time of day and that we found no seasonal effects (e.g., periodic rainfall) impacting on these populations during the study period (Weinstein, 1994; Weinstein and Slaney, 1995), the probability of recording a simultaneous decrease in populations of four different species by chance alone is 0.0625 (0.5⁴). Thus, the data suggest that our sampling of cave invertebrates adversely affected their numbers.

Past studies have also indicated that sampling may have adverse effects on cave populations, with pitfall trapping reducing cave beetle populations (Peck, 1975, 1976). All that may be required to extinguish the local population of a cave dwelling species is the careless or accidental desertion of a pitfall trap (Vandel, 1965; Howarth, 1982). A single trap in a restricted area may not only trap a species to extinction, but may subsequently affect the ecology of the cave itself through changes in the population dynamics of the surviving cave fauna. A possible way of minimising such impacts is to sample with replacement, or if trap sites are to be left in situ for an extended period of time, to use a 'trap' which allows for the free movement of individuals. We have designed a survey tool which meets both of these requirements (Slaney and Weinstein, in press). A wet leaf litter trap (which simulates nutrient influx into dry tropical caves during monsoonal rains) maintains the viability of organisms, thus allowing their release back into the cave environment following identification and counting. Because this trap is not only conservation friendly but is also more effective and more efficient than other sampling techniques (Weinstein and Slaney, 1995), we recommend it as the survey tool of choice in these fragile ecosystems (Slaney and Weinstein, in press).

Implications

Compared with the USA, Australia is extremely depauperate in numbers of caves (Jennings, 1983). Despite this, Australian caves are of international significance, containing a diverse range of cave organisms. Cave habitats in Tasmania are amongst the richest temperate cave communities (Eberhard and Spate, 1995), while tropical caves in Western Australia and

Queensland have an exceptional abundance of cave species (Humphreys, 1993, Howarth, 1988). Legislatively only Tasmania and Western Australia recognises cave invertebrates as important, but even then only on a species by species basis (New, 1984; Eberhard and Spate, 1995; Humphreys, pers. comm.). The formulation of conservation policies/strategies for protecting cave invertebrates is difficult due to the lack of taxonomic and ecological data. The lack of such data is obviously not a problem unique to caves, but is a major shortfall which threatens the conservation of Australia's invertebrate fauna on the whole (New, ms.). Caves more than most other ecosystems can play an important role in making both the public and policy makers aware of this problem, as they tend to have a relatively high local profile (e.g., Jenolan Caves, Undara Lava Tubes, and Chillagoe Caves, all of which are rich in cave fauna and provide important local landmarks).

One of the problems facing cave researchers is determining whether insect species are rare, as they are often difficult to observe due to camouflaging adaptations, the cryptic microhabitats in which they live (cracks or rock piles), and the inaccessibility of the cave in the first place. Further, individuals within each population may be able to find refuges from which they can continually recolonise other cave regions, thus demonstrating patchy distributions both in space (location) and time (seasons). Howarth (1983) stated that there is a requirement for experimental ecological studies to determine what factors limit cave species distribution, what are the significant perturbations, and how these disturbances affect cave communities. For example, long term ecological research is required to establish methodologies for distinguishing between short term population fluctuations and longer term irreversible changes (Howarth and Ramsay, 1991).

Generally, biologists recognised that insect species are endangered to the extent that their habitats are endangered, and that their conservation can be accomplished only by conserving their habitats (Key, 1978). With cave ecosystems the surface and subsurface drainage basins are coupled, forming a highly integrated unit (White *et al.*, 1995), and the conservation of cave fauna would thus be best achieved by protecting the cave ecosystem and the surrounding catchment area (not just around the cave entrance) from the sorts of disturbances we have outlined in this paper (including scientists!). We recommend that ecosystem stability and vulner-

ability to disturbance, as well as the general ecology of organisms in a cave, be considered before any intensive sampling is carried out. We further recommend that any sampling be done with replacement using techniques similar to our own leaf litter traps (Slaney and Weinstein, in press). For cave communities where direct visitation is having an effect on populations of cave species, access must be restricted, and tourism should be established only in caves with few species. Where possible, caves immediately adjacent to such tourist caves should have restricted access to allow organisms to retreat into a readily available refuge.

The faunas of many caves which are under threat either directly or indirectly have not been investigated at all, and may never be discovered without detailed taxonomic and ecological studies. Caves are a unique biological resource with both scientific and cultural importance, especially for invertebrates. We must not neglect the biodiversity and conservation value of these habitats, always bearing in mind that conservation strategies can only be as sound as the research upon which they are based (New, ms.).

References

- Barr, T.C., Jr., 1968. Cave ecology and the evolution of troglobites. *Evolutionary Biology* 2: 35-102.
- Barr, T.C., Jr. and Holsinger, J.R., 1985. Speciation in cave faunas. *Annual Review of Ecology and Systematics* 16: 313-37.
- Caccone, A., 1985. Gene flow in cave arthropods: a qualitative and quantitative approach. *Evolution* 39: 1223-1235.
- Chapman, P., 1993. *Caves and cave life*. Harper and Collins: London.
- Chutter, F.M., 1969. The effects of salt and sand on the invertebrate fauna of streams and rivers. *Hydrobiologia* 34: 57-76.
- Culver, D.C., 1982. *Cave life: evolution and ecology*. Harvard University Press: Cambridge.
- Culver, D.C., 1986. Cave faunas. Pp. 427-443 in: Soulé, M.E. (ed.), *Conservation biology: the science of scarcity and diversity*. Sinauer Assoc.: Sunderland.
- Dexter, E.M. and Kitching, R.L., 1993. The Bathurst Copper, *Paralucia spinifera* Edwards & Common. Pp. 168-170 in: New, T.R. (ed.), *Conservation biology of Lycaenidae (butterflies)*. *Occasional Paper of the IUCN Species Survival Commission* No. 8.
- Eberhard, S. M., 1993. *Survey of fauna and human impacts in the Jenolan caves reserve*. Jenolan Caves Research Trust, NSW.
- Eberhard, S. M., 1995. *Impact of a limestone quarry on aquatic cave fauna at Ida Bay in Tasmania*. NPWS, Hobart.
- Eberhard, S.M., Richardson, A.M.M. and Swain, R., 1991. *The invertebrate cave fauna of Tasmania*. Report to the National Estate Office, Canberra.
- Eberhard, S.M. and Spate, A., 1995. *Cave communities*. NSW NPWS submission to the Endangered Species Unit of the Australian Nature Conservation Agency.
- Hall, L.S. and Dunsmore, J.D., 1974. A survey of cave dwelling bats. *Australian Speleological Federation Newsletter* 64: 9-10.
- Hamilton-Smith, E., 1967. The Arthropoda of Australian caves. *Journal of the Australian Entomological Society* 6: 103-118.
- Hamilton-Smith, E., 1987. Karst creatures: the fauna of Australian karst. *Australian Ranger Bulletin* 4(3): 9-10.
- Heath, A.C.G., 1987. Collect or conserve — the entomologist's dilemma. *New Zealand Entomologist* 9: 4-10.
- Hoch, H. and Howarth, F.G., 1989a. Reductive evolutionary trends in two new cavernicolous species of a new Australian cixiid genus (Homoptera: Fulgoroidea). *Systematic Entomology* 14: 179-196.
- Hoch, H. and Howarth, F.G., 1989b. Six new cavernicolous cixiid planthoppers in the genus *Solonaima* from Australia (Homoptera: Fulgoroidea). *Systematic Entomology* 14: 377-402.
- Howarth, F.G., 1982. The conservation of cave invertebrates. *Proceedings from the International Cave Management Symposium*, Murray, KY, 1981: 57-64.
- Howarth, F.G., 1983. Ecology of cave arthropods. *Annual Review of Entomology* 28: 365-389.
- Howarth, F.G., 1988. Environmental ecology of North Queensland caves: Why there are so many troglobites in Australia. *Australian Speleological Federation 17th Biannual Conference preprints, Lake Tinaroo, December 1988*.
- Howarth, F.G. and Ramsay, G.W., 1991. The conservation of island insects and their habitats. Pp. 71-107 in: Collins, N.M. and Thomas, J.A. (eds), *The conservation of insects and their habitats*. Academic Press: London.
- Howarth, F.G. and Stone, F.D., 1982. The conservation of Hawaii's cave resources. Pp. 94-99 in: Smith, C.W. (ed.), *Hawaii Volcanoes National Park. Proceedings 4th Conference in National Science*. Cooperative National Park Study Unit, University of Hawaii Manoa: Honolulu.
- Howarth, F.G. and Stone, F.D., 1990. Elevated carbon dioxide levels in Bayliss cave, Australia: Implications for the evolution of obligate cave species. *Pacific Science* 44(3): 207-218.
- Humphreys, W.F., 1993. The biogeography of Cape Range Western Australia. *Records of the Western Australian Museum, Supplement* 45.
- Jasinska, E.J. and Knott, B., 1991. The importance of caves at Yanchep, Western Australia. *Proceedings*

- from the 18th Biennial Conference of the Australian Speleological Federation: 55–57.
- Jennings, J.N., 1983. A map of karst cave areas in Australia. *Australian Geographical Studies* 21: 183–196.
- Kane, T.C. and Richardson, R.C., 1985. Regressive evolution: an historical perspective. *National Speleological Society Bulletin* 47(2): 71–77.
- Key, K.H.L., 1978. The conservation status of Australia's insect fauna. *Australian National Parks and Wildlife Service, Occasional Paper* 1.
- Kiernan, K., 1988. *The management of soluble rock landscapes: an Australian perspective*. Speleological Research Council: Sydney.
- Lewis, D.J. and Dyce, A.L., 1983. Phlebotomine sandflies (Diptera: Psychodidae) from caves in Queensland, Australia. *Journal of the Australian Entomological Society* 22: 223–231.
- Lichon, M., 1992. Recent history and issues surrounding the saving of Exit Cave, and future options. *Illuminations* 1: 17–22.
- Lichon, M., 1993. Human impact on processes in karst terranes, with special reference to Tasmania. *Cave Science* 20(2): 55–60.
- Malipatil, M.B. and Howarth, F.G., 1990. Two new species of *Micropolytoxus* Elkins from northern Australia (Hemiptera: Reduviidae: Saicinae). *Journal of the Australian Entomological Society* 29: 37–40.
- Middleton, G.J., 1979. Wilderness caves of the Gordon-Franklin River system. *University of Tasmania, Centre for Environmental Studies Occasional Paper* 11.
- New, T.R., 1984. *Insect Conservation — an Australian perspective*. Dr.W.Junk: Dordrecht.
- New, T.R., ms. Taxonomic focus and quality control in insect surveys for habitat conservation. *Journal of the Australian Entomological Society*.
- Peck, S.B., 1975. A population study of the cave beetle *Ptomaphagus hirtus* (Coleoptera: Leiodidae; Catopinae). *International Journal of Speleology* 7: 303–326.
- Peck, S.B., 1976. The effect of cave entrances on the distribution of cave inhabiting terrestrial arthropods. *International Journal of Speleology* 8: 309–321.
- Pugsley, C., 1984. Ecology of the New Zealand Glowworm, *Arachnocampa luminosa* (Diptera: Keroplatidae), in the Glowworm Cave, Waitomo. *Journal of the Royal Society of New Zealand* 14: 387–407.
- Richards, A., 1971. An ecological study of the cavernicolous fauna of the Nullarbor Plain, Southern Australia. *Journal of the Zoological Society of London* 164: 1–60.
- Roth, L.M., 1990. A revision of the Australian Parcoblattini (Blattaria: Blattellidae: Blattellinae). *Memoirs of the Queensland Museum* 28(2): 531–596.
- Slaney, D.P. and Ragusa, S., 1990. Denitrification in bacterial cultures and soil microcosms. *Centre for Groundwater Studies Report* No. 26, CSIRO: Adelaide.
- Slaney, D.P. and Weinstein, P., in press. Leaf litter traps for sampling orthopteroid insects in tropical caves. *Journal of Orthoptera Research*.
- Spathe, A.P. and Hamilton-Smith, E., 1991. Caver's impacts — some theoretical and applied considerations. *Ninth Akcma Conference*: 20–30.
- Tuttle, M.D., 1979. Status, causes of decline, and management of endangered grey bats. *Journal of Wildlife Management* 43: 1–17.
- Vandel, A., 1965. *Biospeleology*. Translated by B.E. Freeman. Pergamon Press: Oxford.
- Webb, R., 1984. Drovers Cave, Western Australia: cave destruction through management. Pp. 41–48 in: Pilkington, G. (ed.), *Proceedings of the 14th Biennial Conference of the Australian Speleological Federation*. ASF: Sydney.
- Weinstein, P., 1994. Behavioural ecology of tropical cave cockroaches: preliminary field studies with evolutionary implications. *Journal of the Australian Entomological Society* 33: 367–370.
- Weinstein, P. and Slaney, D.P., 1995. Invertebrate faunal survey of Rope Ladder Cave, North Queensland: a comparative study of sampling methods. *Journal of the Australian Entomological Society* 34: 233–236.
- White, W.B., Culver, D.C., Herman, J.S., Kane, T.C. and Mylroie, J.E., 1995. Karst lands. *American Scientist* 83: 450–459.

CONSERVATION OF NATIVE EARTHWORMS AND THE ROLE OF THE GIANT GIPPSLAND EARTHWORM AS A FLAGSHIP TAXON.

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Abstract

Van Praagh, B.D., 1997. Conservation of native earthworms and the role of the Giant Gippsland earthworm as a flagship taxon. *Memoirs of the Museum of Victoria* 56(2): 597-603.

Very little is known of the Australian native earthworm fauna, which has been largely replaced by introduced species in most disturbed areas. The Giant Gippsland Earthworm, *Megascolides australis*, is one of the better known earthworm species and has aroused public curiosity and sympathy due to its gigantism and restricted distribution. The role of *M. australis* as a flagship taxon is discussed in terms of its wider value in the conservation of other earthworm species.

Introduction

Australia has a very diverse indigenous earthworm fauna arising from its long geographical isolation (Lee, 1985), but little detailed information exists on the ecology, distribution or conservation status of any native species (reviewed by Lee, 1985, Kingston and Dyne, 1996). The only species of native earthworm studied in any detail to date is the Giant Gippsland Earthworm, *Megascolides australis* McCoy (Van Praagh, 1992, 1994), the first Australian native earthworm to be described. Most available information regarding native earthworms lies in the taxonomic and biogeographic literature (e.g., McCoy, 1878; Spencer, 1888; Jamieson, 1981; Dyne, 1984; Abbott, 1994). Museum collections are also a valuable source of ecological information on species through the provision of details of habitat or locality data.

Much information on the ecology of earthworms deals primarily with species belonging to the European family Lumbricidae which includes the introduced earthworm species commonly encountered in Australian gardens. The introduced lumbricid *Lumbricus terrestris* Linnaeus, is still commonly used to illustrate a 'typical earthworm' in Australian biology classes and most biology textbooks. Ironically, the existence of this species in Australian soils has yet to be confirmed (R. Blakemore pers. comm. 1995). The assumption that information obtained for lumbricids can be transferred directly to megascolecid is unjustified when the major differences in soils, vegetation types and geological history between Australia and the Northern Hemisphere are considered (Abbott, 1985b).

Wood (1974) stated that 'it is surprising that more is known about the abundance of introduced Lumbricidae in New Zealand and Australia than that of the native Megascolecidae' and more than 20 years later this observation still applies. This paper discusses the conservation status of Australian earthworms and the role of the famous Giant Gippsland Earthworm as a flagship taxon in promoting the conservation of native earthworm fauna.

Australia's earthworm fauna

All Australian native earthworms belong to the family Megascolecidae (Kingston and Dyne, 1996) a mainly southern hemisphere group which occurs over South and Central America, Africa and south-east Asia. Approximately 325 native earthworm species, belonging to 28 genera, have been described from Australia (Kingston and Dyne, 1996). However, knowledge of the indigenous earthworms in different States varies, with the earthworm fauna of Western Australia and the Northern Territory particularly poorly known (Abbott, 1994). For example, only 12 species of earthworms have been described from the Northern Territory (R. Blakemore, pers. comm. 1996). Extrapolation of the number of new species found from recent surveys by Kingston and Dyne (1996) indicate that the number of native earthworm species in Australia is probably well over 1000.

In a recent examination of nearly 2000 museum and literature records, Abbott (1994) mapped the distribution of the native earthworm fauna of Australia and found the major factor limiting earthworm distribution was rain-

fall. Earthworms were generally absent in regions where rainfall was less than 400 mm. However, 30 records of earthworm distribution occurred in areas receiving less than 400 mm. At least 16 of these were found to be surviving under favourable situations such as waterholes, moist caves, permanent rivers and farm dams (Abbott, 1994).

Changes in soil and vegetation resulting from European settlement have led to destruction of some of our indigenous earthworm fauna and to major changes in the distribution and composition of earthworms in Australian soils. In general, native earthworm species do not survive the change from native bush to pasture (Lee, 1961, Wood, 1974) and the predominant family in cultivated soil in southern temperate Australia is the introduced Lumbricidae (Baker et al., 1992a). In disturbed areas of tropical Australia, the native earthworm fauna is largely replaced by a small group of earthworms from the families Glossoscolecidae and Megascolecidae, originally from South and Central America, Africa and south-east Asia (Lee, 1991).

Conservation of earthworms

Vulnerability

Apart from a recent discussion of the conservation of the earthworm fauna of the wet tropics of Queensland by Dyne and Wallace (1994), the conservation status of Australian earthworms is poorly known. Many have extremely limited geographical distributions and may be highly specialised suggesting tolerance to only a narrow range of soil conditions. For example, Dyne (1991a) found *Digaster nothofagi* Jamieson only from a look out in Warrie National Park, Queensland, in apparently uniform and continuous rainforest cover. More recently, Dyne and Wallace (1994) found 45% of new species found in the wet tropics of Queensland's world heritage area from only single sites. The Lake Pedder earthworm, *Diporochoeta pedderensis* Jamieson, was described from a single specimen collected in 1971 from the beach psammon of Lake Pedder in Tasmania. Subsequent searches for the species following the flooding of Lake Pedder in 1972 failed to find any specimens (Dyne, 1991b). Earthworms appear to be highly susceptible to environmental disturbance. In Victoria, The Giant Gippsland Earthworm, *Megascolides australis* is restricted to approximately 40 000 ha of the Bass River Valley and is extremely patchy within this area, being mainly confined to creek banks, gullies and some south

facing slopes. Anecdotal information regarding historical distribution patterns suggests that numbers have declined and the range of the species has contracted through vegetation clearance and farming practices, particularly ploughing (Smith and Peterson, 1981; Van Praagh, 1994). Protection of native earthworms may be particularly important for species that have a restricted distribution or are naturally rare.

Listing of threatened earthworms

Worldwide, three species of giant worms, four genera of South African Acanthodrilinae and two genera of South African microchaetids are listed by the International Union for the Conservation of Nature (IUCN) Invertebrate Red Data Book (Wells et al., 1983). The endemic Acanthodrilinae of South Africa comprise some 90 species, most of which are regarded as threatened (Ljungström, 1972) since they are predominantly litter species restricted to indigenous forests which have been reduced to about 0.3% of their original range for agriculture or exotic plantations (Ljungström, 1972, Wells et al., 1983). *Microchaetus* spp. and *Triogenia* spp. (Microchaetidae) are characteristic of sandy and clayey soils of primary grasslands and savannahs. Agricultural practices have reduced the available areas of suitable habitat by overgrazing, lowering of the water table and desertification of the savannas (Reinecke, 1983, Wells et al., 1983). The microchaetids includes the giant *Microchaetus michrochaetus* Rapp which is thought to be one of the largest earthworms in the world. In Australia, two oligochaetes are documented on threatened species lists. *M. australis* is listed as vulnerable under the Department of Conservation and Natural Resources threatened species list (CNR, 1995) and as threatened under Victoria's *Flora and Fauna Guarantee Act* (1988) (Flora and Fauna Guarantee Scientific Advisory Committee, 1991) and the Lake Pedder earthworm is listed as endangered under the Tasmanian rare or threatened species list (Invertebrate Advisory Committee, 1994), but is thought to be extinct.

Threats to earthworms

Vegetation Clearance. Since European settlement, there has been complete conversion of whole land systems to the growing of wheat and improved pastures (Frood and Calder, 1987). Native earthworms are rarely found in cultivated soils (Wood, 1974; Abbott and Parker, 1980, Baker et al., 1992a, b, 1995; Kingston and Temple-Smith, 1988; Tisdall, 1985; Mele,

1991). The conversion of land systems to cane farming in Queensland is thought to have resulted in the extinction of some earthworm species (Wells et al., 1983).

Reasons for the disappearance of native earthworms after cultivation are unknown but may be linked to the shift in the microclimate with clearing of native vegetation and establishment of pasture (Baker et al., 1992b; Kingston and Dyne, 1996). This includes changes in sunlight, soil temperature and moisture, removal of food sources (particularly important for surface feeders), disruption of burrow systems, altered soil pH and fertility and the use of chemicals such as pesticides. Changes in soil microflora, with which some native species have a symbiotic relationship, may also be important (Kingston and Dyne, 1996). Most native earthworms do not survive the initial cultivation process such as conversion of native vegetation to pasture and the direct effects of cultivation on earthworms are mainly from studies on introduced earthworms.

Survival of species in Agricultural Land

Some species of native earthworms can persist in cultivated soils. In a study of the earthworm fauna of the northern jarrah forest of Western Australia, Abbott (1985b) found indigenous species both in little disturbed and grossly disturbed sites. Baker (1996) and Mele (1991) found native species of *Spenceriella* Michaelsen and *Heteroporodrilus* Jamieson to predominate in many pastures in western Victoria. A native megascolecid, *Gemascolex walkeri* Jamieson, was found occasionally to constitute a substantial proportion of the total earthworm population in pasture soils of the Mt Lofty Ranges with densities reaching up to 108 per m² (Baker et al., 1993). Cultivation has actually appeared to create a favourable environment for the indigenous megascolecid *Megascolex imparicystis* Michaelsen which is more abundant under cultivated areas and clovered pastures than in its natural habitat of undisturbed bush (Abbott et al., 1985).

While there have been no detailed studies examining why some indigenous species can survive disturbance such as vegetation clearance, one reason may be a consequence of the specific ecological niche occupied by the species. Several studies have shown that subsoil species generally have the best chance of survival in comparison to litter and top soil species when native vegetation is converted to pasture (Lee, 1961; Wood, 1974; Miller et al., 1955 in Lee, 1985;

Dyne, 1991a). For example, the giant rainforest species *Digaster longmani* Boardman, found at depths of 0.8–1.5 m, is occasionally reported from areas where its original rainforest vegetation has been completely removed and is now used for cultivation or housing (Dyne, 1991a). Non selectivity usually associated with the geophagous diet of subsoil species has been implicated as a factor in allowing this species to survive habitat alteration (Dyne, 1991a). Geophagous species feed in the deeper soil horizons and ingest large quantities of soil, in contrast to detritivores which feed mainly on plant litter, dead roots and other plant debris at or near the soil surface. Therefore, when the natural vegetation is cleared, there is a major change in the nature and quantity of the major food source available to detritivores. Similarly, Ljungström and Reinecke (1969) and Reinecke (1983) found that only a few of the large endemic subsoil microchaetids survived the cultivation of South African soils, though their range has contracted. In contrast the litter dwelling Acanthodrilinae under the same conditions have almost totally disappeared.

Clearly small amounts of remnant vegetation will be important for the survival of some native species in agricultural land. For example, clearing of native vegetation on areas occupied by *M. australis* took place between the 1870s and the 1930s. Even though the extent of suitable habitat for *M. australis* has been reduced, the worm has been able to survive in highly altered circumstances in refuge areas such as stream banks, roadsides and gullies where the effects of cultivation have been less severe. In several cases where the species was found along roadsides, its distribution did not extend into the adjacent paddocks (Van Praagh, 1994). Survival of species along stream banks and road sides may be partly encouraged as a result of remnant native vegetation still found in these areas. Buckerfield (1992) found native earthworms persisting under native vegetation on roadsides but not in fields under crops and attributed this partly to the availability of food. Baker et al. (1993) suggested the existence of some remnant *Eucalyptus* in one corner of a pasture site in the Mount Lofty Ranges, South Australia, may be responsible for local survival of the native *Gemascolex lateralis* Spencer. Buckerfield (1993) has shown that even if some indigenous earthworms survive cultivation or clearing, other factors such as the addition of fungicides may contribute to their decline. In South Australian pastures, the native species *Gemascolex*

walkeri Jamieson survived clearing of its original habitat until a single application of the fungicide Benomyl was made. This resulted in a marked reduction of *G. walkeri* numbers with introduced species becoming more abundant (Buckerfield, 1993).

Threats from introduced species?

Approximately 50 species of exotic earthworms have been recorded from Australia (R. Blakemore, pers. comm. 1995). Most exotic species are from accidental introductions, primarily from soil in potted plants (Lee, 1985). Distribution of introduced earthworms in Australia is patchy, reflecting chance introductions and different species predominate in different regions (Baker et al., 1992b; Baker and Mele, 1996). Much earthworm research in Australia is focused on trying to establish appropriate exotic species in cultivated land to improve productivity. This has led to the suggestion of translocation of exotic earthworm species from a) other regions of Australia and b) overseas (Lee, 1985; Rovira et al., 1987; Baker et al., 1992b, 1996). The two most popular earthworms used in worm farming include the Tiger worm *Eisenia fetida* (Savigny) and the Red worm *Lumbricus rubellus* Hoffmeister both introduced species, which are primarily used in composting.

Little is known about the invasion of native habitats by introduced species already in Australia. Although most introduced species are confined to disturbed areas, some have invaded native vegetated areas. Dyne and Wallace (1994) expressed concern at the presence of the exotic *Pontoscolex corethrurus* (Müller) in primary forest in Queensland. This species is a vigorous coloniser which may pose a threat to the indigenous species since native species rarely coexist with *P. corethrurus*. Dyne and Wallace (1994) suggested that the colonising species may inhibit reinvasion by native species through chemical interference or changes in soil structure.

It is not always clear whether native or introduced species are involved in introductions or translocations for soil improvement. For example, one earthworm commonly used by worm breeders is known as 'the Blue' or 'Indian Blue'. This species is usually sold as the exotic species *Perionyx excavatus* (Perrier) but it has recently been identified (Murphy, 1993) as a native species of *Spenceriella*. The introduced *Aporrectodea caliginosa* (Savigny), recommended for use in increased pasture productivity, is described as an indigenous

earthworm by Windust (1994). The vigorous *Pontoscolex corethrurus*, already shown to invade undisturbed areas, is also promoted by worm breeders as a pasture species for tropical pastures and croplands (Windust, 1994). Exotic species and possibly some native species are being moved around Australia through worm farming and breeding. At present, there are no controls in place and little monitoring of what species are being released and where.

While studies suggest that exotic species are mainly confined to disturbed areas and there is little evidence of competition between introduced and native species, very little detailed data exist on the indigenous species that do survive clearing or the effects on native earthworms of those exotics that can invade undisturbed areas. Some of these issues are currently being addressed (G. Baker, pers. comm. 1995). However, until more information is available on these issues, caution should be taken in the redistribution of introduced earthworm species and priority given toward the formulation of guidelines and monitoring procedures regulating the industry.

Flagship taxa

Not all invertebrates are equal in their ability to elicit public sympathy or concern for their welfare. Flagship taxa, also termed 'attention grabbers' by Towns and Williams (1993), are recognised as those taxa that are either charismatic or popular and are used to initiate awareness and draw attention to the wider role of invertebrates as serious components of the ecosystem. *M. australis* is one of the most famous members of Australia's endemic fauna due to its gigantic size. The species is restricted to a small area of the Bass River Valley in South Gippsland, Victoria. Even though *M. australis* has been known for over one hundred years and was recognised as vulnerable by the IUCN in 1983, recent studies (Yen et al., 1990; Van Praagh, 1992, 1994) represent the first efforts to address the conservation and management issues of an earthworm.

M. australis is an excellent example of a flagship taxon and fulfils most of the desirable features of flagship taxa outlined by New (1991). Those relevant to *M. australis* include:

1. taxonomy well known and easily identifiable;
2. ability to elicit public sympathy and appeal;

3. occurrence in areas where other aspects of conservation are a concern (e.g., conserving the unknown biodiversity of the soil fauna by aiming to conserve what is already a diminishing habitat);
4. the actual or potential threatening processes can be identified and response of taxon monitored; and
5. facility to influence conservation policy.

M. australis is a charismatic species that has aroused public curiosity and sympathy primarily due to its novelty value as a giant and its localised distribution. Adult worms obtain lengths of over 1 m and weigh up to 400 g (Van Praagh, 1994). This has aroused pride in the local community in which the worm occurs, to the extent that a festival is held each year in its honour. The local shire has sponsored a static exhibit of the species in its underground habitat at the Coal Creek Historical Park, a major tourism focus in the area. The interest generated by this species has raised the awareness of invertebrates to local Department of Conservation and Natural Resource officers who help to record sightings of the species and have helped influence government policy to protect the worm. The Land for Wildlife scheme was developed to encourage private land owners to conserve wildlife on their properties and several local farmers are involved in conserving stream banks, the primary habitat of *M. australis*, by fencing off stock and replanting stream banks with indigenous vegetation. A pamphlet with management guidelines for *M. australis* (Van Praagh, 1991), is distributed through local land care groups and extension programs. The interest generated in this study both nationally and internationally through various television shows, radio interviews and newspaper and magazine articles served to raise the awareness of the role of earthworms in the environment and the importance of their conservation.

Species such as *M. australis* can be used to highlight the role of earthworms in the environment and increase the interest in the conservation of Australia's native earthworm fauna. With probably only one quarter of Australia's indigenous earthworm fauna described and the conservation status of only two earthworms known, it is clear that much greater attention should be given to native earthworm research to gain a clearer understanding of the conservation needs of earthworms. *M. australis* could be used to generate awareness of the conservation issues facing native earthworms, including the unresolved issues of unregulated worm farming and

earthworm translocation within Australia. Indeed worm farming may present an excellent opportunity for promoting earthworm conservation.

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References

- Abbott, I., 1985a. Influence of some environmental factors on indigenous earthworms in the northern jarrah forest of Western Australia. *Australian Journal of Soil Research* 23: 271–290.
- Abbott, I., 1985b. Distribution of introduced earthworms in the northern jarrah forest of Western Australia. *Australian Journal of Soil Research* 23: 263–270.
- Abbott, I., 1994. Distribution of native earthworms in Australia. *Australian Journal of Soil Research* 32: 117–126.
- Abbott, I. and Parker, C.A., 1980. The occurrence of earthworms in the wheat-belt of Western Australia in relation to land use and rainfall. *Australian Journal of Soil Research* 18: 343–352.
- Abbott, I., Ross, J.S. and Parker, C.A., 1985. Ecology of the large indigenous earthworm *Megascolex imparicystis* in relation to agriculture near Lancelin, Western Australia. *Journal of the Royal Society of Western Australia* 68(1): 13–15.
- Baker, G.H., 1996. Introduction of earthworms to agricultural soils in southern Australia. In: Temple-Smith, M.G. and Pinkard, T. (eds), *The role of earthworms in agriculture and land management*. Report of the National Workshop held in Launceston, Tasmania. Department of Primary Industry and Fisheries, Tasmania.
- Baker, G.H., Barrett, V.J., Grey-Gardener, R. and Buckerfield, J.C., 1992a. The life history and abundance of the introduced earthworms *Aporrectodea trapezoides* and *A. caliginosa* (Annelida: Lumbricidae) in pasture soils in the Mount Lofty Ranges, South Australia. *Australian Journal of Ecology* 17: 177–188.
- Baker, G.H., Buckerfield, J.C., Grey-Gardener, R., Merry, R. and Doube, B., 1992b. The abundance and diversity of earthworms in pasture soils in the Fleurieu Peninsula, South Australia. *Soil Biology and Biochemistry* 24(12): 1389–1396.
- Baker, G.H., Barrett, V.J., Grey-Gardener, R. and Buckerfield, J.C., 1993. Abundance and life history of native and introduced earthworms (Annelida: Megascolecidae and Lumbricidae) in pasture soils in the Mount Lofty Ranges, South Australia. *Transactions of the Royal Society of South Australia* 117: 47–53.

- Baker, G.H. and Mele, P., 1996. Introduced species: populations and distribution in agricultural land. In: Temple-Smith, M.G. and Pinkard, T. (eds), *The role of earthworms in agriculture and land management*. Report of the National Workshop held in Launceston, Tasmania. Department of Primary Industry and Fisheries, Tasmania.
- Buckerfield J.C., 1992. Earthworm populations in dryland cropping soils under conservation-tillage in South Australia. *Soil Biology and Biochemistry* 24: 1667–1674.
- Buckerfield, J.C., 1993. Long-term responses of native and introduced earthworms to pasture soil applications of fungicides. Pp. 92–99 in: Prestige, R.A. (ed.), *Proceedings of the 6th Australasian Grassland Invertebrate Ecology Conference 1993*. Agresearch: Hamilton, New Zealand.
- CNR, 1995. *Threatened fauna in Victoria — 1995*. Department of Conservation and Natural Resources, Victoria.
- Dyne, G.R., 1984. *Systematics and zoogeography of Australian megascolecoïd earthworms*. Ph.D. Thesis, University of Queensland.
- Dyne, G.R., 1991a. Earthworm fauna of Australian Rainforests. In: *The rainforest legacy Volume 2. Special Publication of the Australian Heritage Commission* 7(2): 335–343.
- Dyne, G.R., 1991b. *The status of the Lake Pedder earthworm, Perionychella pedderensis and investigations into new or little-known earthworms from the Western Tasmania World Heritage Area*. Unpublished report to the Department of Parks, Wildlife and Heritage. 18 pp.
- Dyne, G.R. and Wallace, C.C., 1994. Biodiversity and conservation of the earthworm fauna of the wet tropics of Queensland's World Heritage area. *Memoirs of the Queensland Museum* 36(1): 59–66.
- Frond, D. and Calder, M., 1987. *Nature Conservation in Victoria Study Report. Volume 1*. Victoria National Parks Association: Melbourne.
- Invertebrate Advisory Committee, 1994. *Interim list of native invertebrates which are rare or threatened in Tasmania*. Parks and Wildlife Services, Tasmania.
- Jamieson, B.G.M., 1981. Historical biogeography of Australian Oligochaeta. Pp. 887–920 in: Keast, A. (ed.), *Ecological biogeography in Australia*. Dr. W. Junk: The Hague.
- Kingston, T.J. and Dyne, G., 1996. Potential for agronomic exploitation of Australian native earthworms. In: Temple-Smith, M.G. and Pinkard, T. (eds), *The role of earthworms in agriculture and land management*. Report of the National Workshop held in Launceston, Tasmania. Department of Primary Industry and Fisheries, Tasmania.
- Kingston, T.J. and Temple-Smith, M.G., 1988. Earthworm populations under Tasmania pastureland. Pp. 192–198 in: Stahle P.P. (ed), *Proceedings of the 5th Australasian Conference on Grassland Invertebrate Ecology*. Melbourne.
- Lee, K.E., 1961. Interactions between native and introduced earthworms. *Proceedings of the New Zealand Ecological Society* 8: 60–62.
- Lee, K.E., 1985. *Earthworms: their ecology and relationship with soils and land use*. Academic Press.
- Lee, K.E., 1991. The Diversity of Soil Organisms. Pp. 73–87 in: Hawksworth, D.L. (ed.), *The biodiversity of micro-organisms and invertebrates: its role in sustainable agriculture*. CAB International.
- Ljungström, P. O., 1972. Introduced earthworms of South Africa. On their taxonomy, distribution, history of introduction and on the extermination of endemic earthworms. *Zoologische Jahrbücher Systematik* 99: 1–81.
- Ljungström, P.O. and Reinecke, A., 1969. IV. Studies on influences of earthworms upon the soil and the parasitological questions. *Pedobiologia* 9: 152–157.
- McCoy F., 1878. *Megascolides australis* (McCoy). The giant earthworm. *Prodromus to the Zoology of Victoria* 1: 21–25.
- McKenzie, N.L. and Dyne, G.R., 1991. Earthworms of rainforest soils in the Kimberley, Western Australia. Chapter 7. Pp. 133–144 in: McKenzie N.L., Johnson R.B., and Kendrick P.G. (eds), *Kimberley rainforests*. Surry Beatty and Sons: Chipping Norton, NSW.
- Mele, P.M., 1991. What species, and how many, on local farms? Pp. 23–29 in: *Earthworms: Improving Soil for Agriculture. Proceedings of a Conference, Wangaratta, September 1991*.
- Murphy, D., 1993. *Earthworms in Australia. A blueprint for a better environment*. Hyland House: South Melbourne.
- New, T.R., 1991. Swallowtail butterflies as flagships for insect conservation. *News Bulletin Entomological Society Queensland* 19(7): 95–107.
- Reinecke, A.J., 1983. The ecology of earthworms in southern Africa. Pp. 195–207 in: Satchell, J.E. (ed.), *Earthworm ecology from Darwin to vermiculture*. Chapman and Hall.
- Rovira, A.D., Smettem, K.R.J. and Lee, K.J., 1987. Effect of rotation and conservation tillage on earthworms in a red-brown earth under wheat. *Australian Journal of Agricultural Research* 38: 829–834.
- Scientific Advisory Committee, Flora and Fauna Guarantee (SAC), 1991. *Final recommendation on a nomination for listing: Megascolides australis* (McCoy 1878) — *Giant Gippsland Earthworm*. (Nomination No. 136). Department of Conservation and Environment, Victoria.
- Smith, B.J. and Peterson J.A., 1982. Studies of the Giant Gippsland Earthworm *Megascolides australis* McCoy, 1878. *Victorian Naturalist* 99: 164–173.
- Spencer, W.B., 1888. On the anatomy of *Megascolides australis*, the Giant Earthworm of Gippsland. *Transactions of the Royal Society of Victoria* 1: 3–60.

- Tisdall, J.M., 1985. Earthworm activity in irrigated red-brown earths used for annual crops in Victoria. *Australian Journal of Soil Research* 23: 291–299.
- Towns, D.R. and Williams, M., 1993. Single species conservation in New Zealand: towards a redefined conceptual approach. *Journal of the Royal Society of New Zealand*. 23(2): 61–78.
- Van Praagh, B.D., 1991. Giant Gippsland Earthworm — 'Nature's Plough.' *Land for Wildlife Note No. 11*. Department of Conservation and Environment.
- Van Praagh, B.D., 1992. The biology and conservation of the Giant Gippsland earthworm *Megascolides australis* McCoy, 1878. *Soil Biology and Biochemistry* 24 (12): 1363–1368.
- Van Praagh, B.D., 1994. *The biology and conservation of the Giant Gippsland Earthworm Megascolides australis* McCoy, 1878. PhD Thesis, La Trobe University, Bundoora.
- Windust, A., 1994. Worms downunder for farm, garden, schools, profit and recycling. Allscape, Victoria.
- Wells, S. M., Pyke, R. M. and Collins, N. M., 1983. *The IUCN Invertebrate Red Data Book*. IUCN: Gland, Switzerland.
- Wood, T.G., 1974. The distribution of earthworms (Megascolecidae) in relation to soils, vegetation and altitude on the slopes of Mt Kosciusko, Australia. *Journal of Animal Ecology* 43: 87–106.
- Yen A.L., New, T. R., Van Praagh B.D. and Vaughan P.J., 1990. Invertebrate Conservation: three case studies in southeastern Australia. Pp. 207–224 in: Clark, T. and Seebeck, J.H. (eds), *Management and conservation of small populations*. Brookfield.

COMPILATION OF A LIST OF THREATENED INVERTEBRATES: THE TASMANIAN EXPERIENCE.

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Abstract

Taylor, R.J. and Bryant, S.L., 1997. Compilation of a list of threatened invertebrates: the Tasmanian experience. *Memoirs of the Museum of Victoria* 56: 605–609.

The Invertebrate Advisory Committee was convened in 1992 to produce a list of rare and threatened non-marine invertebrates for Tasmania. The interim list, completed in 1994, was prepared for inclusion in threatened species legislation and to ensure consideration was given to invertebrates in forest harvesting operations. 175 species from seven phyla, eight classes and 25 orders were listed according to IUCN categories. In some cases entire taxonomic groups had to be ignored due to lack of information, hence the interim status of the list and the need for regular review. Some of the problems encountered during the compilation of the list are outlined. Lists of threatened species can be used as a tool to further other habitat, ecosystem or multi-species approaches to invertebrate conservation.

Invertebrate Advisory Committee

The Invertebrate Advisory Committee was convened by the Tasmanian Parks and Wildlife Service in August 1992 to compile a list of rare and threatened terrestrial and aquatic invertebrates for Tasmania. The stimulus for the production of such a list was provided by the recommendation of the RAVES (Rare, Vulnerable and Endangered Species) Working Group that legislation be introduced which protected threatened species on all land tenures in Tasmania. The Invertebrate Advisory Committee was composed of eight representatives drawn from the University of Tasmania, government departments, the two Tasmanian Museums and a private consultant. Members were chosen for their knowledge of Tasmania's native invertebrates and their ability to critically evaluate the conservation status of a species.

The review process

The Committee reviewed all native terrestrial and freshwater invertebrates in Tasmania, excluding Macquarie Island (due to insufficient information). Marine invertebrates were not included because they are defined under the *Living Marine Resources Act 1995* and hence are the responsibility of the Sea Fisheries section of the Department of Primary Industries and Fisheries. Each member of the committee was given several groups of invertebrates to assess. For insects, orders were the unit of grouping whereas whole phyla were allocated for the remaining

invertebrates. These groups of invertebrates were allocated to members of the committee on the basis of their knowledge of the group whilst trying to equalise the work load. The paucity of knowledge on some groups, for example mites and nematodes, precluded their consideration.

Each committee member was responsible for compiling data on the status of species in the groups they were allocated. Information was obtained from Australian and overseas specialists, from published sources and from their own unpublished material. All species that had been listed as being rare or threatened in other compilations (Wells et al., 1983; Hill and Michaelis, 1988; Smith, 1989) were targeted. Once the compilation of information for a group had been completed it was presented to the committee for its consideration. The status of some species was unanimously agreed upon whilst for others a majority decision decided their categorisation.

Assessing rarity

The problem of deciding when to classify a species as rare was considered by the Committee before any species were categorised. Two categories of rarity were devised as working definitions. The first included species that were widespread, but never abundant, and possessed ecological characteristics which put them at risk. The second included species that were well researched and known to occur in 10 or fewer 1 km grid squares. The level of research work which was considered sufficient for the latter definition was left open to interpretation by

individual specialists based on their knowledge of the group and its ecology. As work progressed it was found that the definitions of rarity had to be used flexibly in conjunction with an assessment of survey effort. The distribution and ecological requirements of some species were well known and the two categories could be applied easily. However, for most species some interpretation of the distribution data had to be made in the light of survey effort. An example of the known locations of five species of caddisflies are shown in Fig. 1. Each species was known from only one or two locations. However, access into the area between the two locations (Cradle Mountain and a tributary of the Gordon River) where *Poecilochorema lepnevae* was found was difficult and most of this area had not been sampled. For the other species in Fig 1, however, there was good access and areas around the known locations had been sampled.

For one group, the hydrobiid snails, the rarity category was accepted as being appropriate despite the fact that the distributions of species were not known in detail. Work by Ponder et al. (1994) on Wilsons Promontory in Victoria had shown that these snails showed high levels of

local endemism with very low rates of gene flow between catchments. It was therefore likely that species exhibiting small distributions from the work of Ponder et al. (1993) would not have their distributions increased substantially by further survey work.

Unpublished information from experts

Unpublished information and opinions on the status of species was sought from experts on particular groups or species. However, opinions of experts were not accepted outright. The data were always assessed independently by the committee. Taxonomic opinion was also required to be assessed when it affected the status of a species. Thus one submission to the committee argued that a certain named species should not be included as it was synonymous with another more widely distributed species. The committee debated whether this information should be accepted without having gone through the normal scientific review process. After further detailed reasoning was requested from the expert the committee decided to accept his opinion.

Risk codes

The committee began assessing the conservation status of species according to the IUCN Red Data categories from 1990 (i.e. rare, vulnerable, endangered, extinct). During this assessment process the IUCN released several discussion papers relating to a revision of threatened species categories. One of these (Mace et al. 1992) included the new category 'susceptible' for species which did not qualify in the higher categories of threat but whose status was of concern because of a restricted range (typically less than 100 km) and/or being found at few locations which rendered it prone to human disturbance. The Committee considered the 'susceptible' category as an ideal classification for many invertebrate species which had small ranges but were not obviously threatened. Many species previously classified as rare were therefore reclassified as susceptible. However, in the next revision of the IUCN categories (Mace and Stuart, 1994), which were subsequently adopted by the IUCN Species Survival Commission (1994), the susceptible category was subsumed into the vulnerable category. However, because the foreshadowed Tasmanian legislation included a 'rare' category it was felt that in our listing these two categories should not be amalgamated. Thus our rare category included

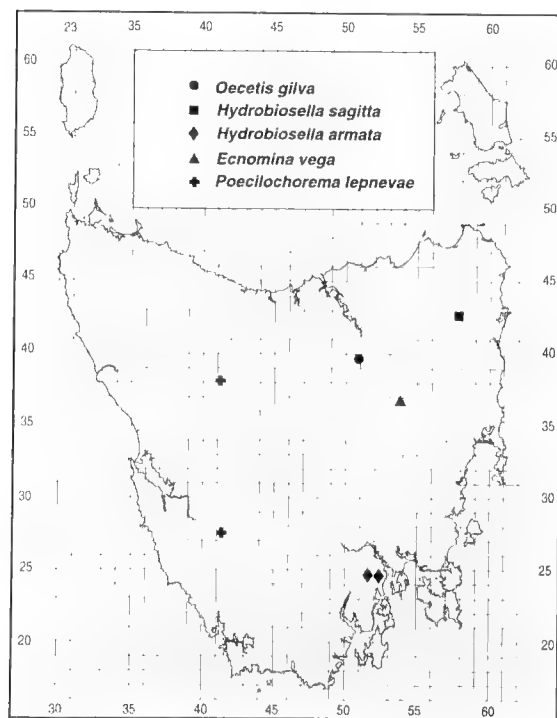


Figure 1. Known locations for five species of caddisflies. Adapted from Neboiss (1977).

species that were very uncommon but widespread and those with very small or restricted populations that were mostly contained within reserves. The criteria for our vulnerable category were as for IUCN Species Survival Commission (1994) with the exclusion of criteria D. Those meeting the criteria D of the vulnerable category of the new IUCN system and whose distributions were mostly outside of reserves were classified as rare (susceptible) under our system. The other categories were the same as that used in IUCN Species Survival Commission (1994).

The list and its uses

An interim list of rare and threatened invertebrates for Tasmania was published in August 1994 (Invertebrate Advisory Committee, 1994). To our knowledge this is the first time that an attempt has been made to comprehensively examine the conservation status of a state's native invertebrates. The list was titled as 'interim' to emphasise the fact that only a relatively small proportion of Tasmania's non-marine invertebrates were able to be considered. Table 1 summarises the listed species according to taxonomic groups. In total 175 species from seven phyla, eight classes and 25 were included.

To date the list has been used for three major purposes. The first two relate to forest management. A compilation of the locations of rare and threatened species associated with forest has been produced as a manual by Forestry Tasmania (Jackson and Taylor, 1995). Released in January 1995 the manual is now used widely by Forestry officers to assess whether a rare or threatened species is known or likely to occur in areas to be logged. By the end of October 1995 42 cases involving known or suspected locations for rare or threatened species were reported from State forest and private land. Nine species were involved with 69% of cases related to two species. The biodiversity component of the Comprehensive Regional Assessment for Tasmania's Regional Forest Agreement (Commonwealth of Australia, 1995) has specifically targeted rare and threatened invertebrates associated with forest. Functional groups with an obvious predominance on the list, such as burrowing crayfish, aquatic snails, troglobites and log dwelling beetles, have been targeted for the preparation of thematic management prescriptions.

The second purpose of the list has been to provide the basis of a schedule of rare and threatened invertebrates included on Tasmania's *Threatened Species Protection Act* proclaimed in November 1995. The Act, however,

Table 1. Summary of rare and threatened native invertebrates in Tasmania.

Group	Extinct	Endangered	Vulnerable	Rare (susceptible)	Rare	Total
Oligochaeta	1	-	-	-	1	
Arachnida	2	-	-	5	613	
Malacostraca	-	1	4	12	4	21
Mollusca						
Terrestrial	1	-	2	2	6	11
Aquatic	-	-	2	41	7	50
Onychophora	-	1	-	2	-	3
Cestoda	-	-	1	-	-	1
Chilopoda	-	-	-	3	-	3
Insecta						
Coleoptera	1	1	5	3	1	11
Lepidoptera	1	1	4	3	2	11
Orthoptera	-	1	-	2	4	7
Plecoptera	-	-	-	1	4	5
Trichoptera	2	2	-	12	18	34
Others	-	-	-	-	4	4
Total	8	7	18	86	56	175

did not include the non-susceptible category of the rare species nor the twenty-two undescribed species from the interim list as it was considered to be politically and/or legally unwise. A Scientific Advisory Committee is to be established within the Act to oversee the listing and delisting process. It is likely that upon appointment this committee will review the complete list. It is envisaged that the Invertebrate Advisory Committee will most likely continue the assessment and revision of the list and make recommendations to the Scientific Advisory Committee.

Production of the list has already stimulated research. A spider previously thought extinct, *Plesiothele fentoni*, has been rediscovered and detailed survey work on the velvet worm *Ooperipatellus 'cryptus'* and the snail *Anoglypta launcestonensis*, that was stimulated by the listing of these species, has led to recommendations that these species be delisted (R. Mesibov and K. Bonham, pers. comm.). Surveys of two log-dwelling beetles (*Lissotes menalcus*, and *Hoplogonus simsoni*) are currently being undertaken and have led to interim protection measures being implemented for the latter species.

Value of the listing process

Tasmania's interim list of rare and threatened invertebrates represents a significant starting point in highlighting the magnitude of invertebrate biodiversity in Tasmania. Previously only high profile or 'glamour' invertebrates, such as the giant freshwater crayfish *Astacopsis gouldi* and the butterfly *Oreixenica ptunarra*, had been used to increase awareness of invertebrates in the community or to attract funding through the federal Recovery Plan process. The list has highlighted the diversity of invertebrates and, although short (0.6% of a possible 30 000 species, Greenslade, 1985), highlights the paucity of information and the need for further surveys and taxonomic research. To date very little funding has been provided by the Endangered Species Unit of the Australian Nature Conservation Agency for invertebrate conservation. However, production of lists such as this should assist with lobbying to remedy this funding imbalance and assist in expediting the inclusion of invertebrates on the schedule of the national *Endangered Species Protection Act* 1992.

Single species versus multi-species or habitat conservation

The listing and recovery plan process for single species of invertebrates has been questioned by Yen and New (1995) because they see it as being ineffective given the large number of invertebrates which could potentially swamp such a system. They argue for a habitat or species assemblage approach. We agree that such broader strategies are extremely important. However, we would argue that the best way to go about achieving the political recognition of the need for such strategies is through the listing of single species. The single species approach has been accepted and legislated for throughout all Australian states. If the view that 'we need more data' (e.g. see Yen and Butcher (1992) and Greenslade (1992) for a reply), is continued to be espoused as the major way forward then we believe invertebrate conservation will continue to be ignored by funding agencies. The listing of species in itself does not necessarily improve an invertebrate's chance of survival, as demonstrated by the experience with the United States *Endangered Species Act* 1973 (Losos, 1993). However, such listings have been used successfully to achieve reservation of significant remnant habitats in the US (Hafernik, 1992). Such remnant habitats are sometimes too small to support viable populations of vertebrates but can be important refuges for invertebrates and plants (Main, 1987; Wilson, 1987).

In the short time since the listing of threatened invertebrates in Tasmania we have seen a dramatic increase in the profile and level of conservation research carried out on this group. So far only those species that are listed have been the focus of attention. However, because of the presence of certain groups of species on the list, we have been able to focus attention on to habitats that seem to be important for threatened invertebrates (e.g. decaying logs, caves) or functional groups that are particularly at risk (e.g. aquatic snails, log-dwelling beetles). A review of the US experience lead to the recommendation that more emphasis be placed on multi-species and ecosystem-level recovery plans (Tear et al., 1995). We believe that the pressure that is required to gain acceptance at a political level for the need for such work will come from the fact that the case can be argued on the basis of

species that are listed as threatened. Such lists are not a panacea, however, and must be seen as only one of many tools that should be used to achieve the conservation of invertebrates.

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References

- Commonwealth of Australia, 1995. *Commonwealth environmental and heritage obligations and assessments relevant to the Regional Forest Agreement process*. Information Paper. Commonwealth of Australia: Canberra.
- Greenslade, P., 1985. *Conservation priorities in Tasmanian non-marine invertebrates*. Tasmanian National Parks and Wildlife Service, Hobart.
- Greenslade, P., 1992. Invertebrate action. *Search* 23: 229.
- Hafernik, J.E., 1992. Threats to invertebrate biodiversity: implications for conservation strategies. Pp. 171–195 in: Fiedler, P.L. and Jain, S.K. (eds), *Conservation biology: the theory and practice of nature conservation*. Chapman and Hall: New York.
- Hill, L. and Michaelis, F.B., 1988. *Conservation of insects and related wildlife*. ANPWS Occasional Paper. No. 13.
- Invertebrate Advisory Committee, 1994. *Interim list of native invertebrates which are rare or threatened in Tasmania*. Parks and Wildlife Service: Hobart.
- IUCN, 1990. *1990 IUCN Red List of threatened animals*. IUCN: Gland.
- IUCN Species Survival Commission 1994. *IUCN Red List categories*. IUCN: Gland.
- Jackson, J. and Taylor, R. J., 1995. *Threatened fauna manual for production forests in Tasmania*. Forestry Tasmania: Hobart.
- Losos, E. 1993. The future of the US Endangered Species Act. *Trends in Ecology and Evolution* 8: 332–336.
- Mace, G., Collar, N., Cooke, J., Gaston, K., Ginsberg, J., Leader Williams, N., Maunder, M. and Milner-Gulland, E.J., 1992. The development of new criteria for listing species on the IUCN Red List. *Species* 19: 16–22.
- Mace, G.M. and Stuart, S.N., 1994. Draft IUCN Red List categories, version 2.2. *Species* 21–22: 13–24.
- Main, B.Y., 1987. Persistence of invertebrates in small areas: Case studies of trapdoor spiders in Western Australia. Pp. 29–39 in: Saunders, D.A., Arnold, G.W., Burbidge, A.A. and Hopkins, A.J.M. (eds), *Nature conservation: the role of remnants of native vegetation*. Surrey Beatty & Sons: Sydney.
- Neboiss, A., 1977. A taxonomic and zoogeographic study of Tasmanian caddis-flies (Insecta: Trichoptera). *Memoirs of the National Museum of Victoria* 38: 1–208.
- Ponder, W.F., Clark, G.A., Miller, A.C. and Toluzzi, A., 1993. On a major radiation of freshwater snails in Tasmania and eastern Victoria: a preliminary overview of the *Beddomeia* group (Mollusca : Gastropoda : Hydrobiidae). *Invertebrate Taxonomy* 7: 501–750.
- Ponder, W.F., Colgan, D.J., Clark, G.A., Miller, A.C. and Terzis, T., 1994. Microgeographic, genetic and morphological differentiation of freshwater snails — the hydrobiidae of Wilsons Promontory, Victoria, south-eastern Australia. *Australian Journal of Zoology* 42: 557–678.
- Smith, S., 1989. Conservation of Tasmanian land animals. Pp. 11–12 in: Fensham, R. (ed.), *Threatened species and habitats in Tasmania*. Centre for Environmental Studies, University of Tasmania: Hobart.
- Tear, T.H., Scott, J.M., Hayward, P.H. and Griffith, B., 1995. Recovery plans and the Endangered Species Act : are criticisms supported by data? *Conservation Biology* 9: 182–195.
- Wilson, E.O., 1987. The little things that run the world. *Conservation Biology* 1: 344–346.
- Yen, A.L. and Butcher, R., 1992. Practical conservation of non-marine invertebrates. *Search* 23: 103–105.
- Yen, A.L. and New, T.R., 1995. Some problems affecting implementation of recovery programmes for threatened Australian non-marine invertebrates species. Pp. 9–14 in: Bennett, A., Backhouse, G. and Clark, T. (eds), *People and nature conservation. Perspectives on private land use and endangered species recovery*. Royal Zoological Society of NSW: Sydney.
- Wells, S.M., Pyle, R.M. and Collins, N.M. 1983. *The IUCN Invertebrate Red Data Book*. IUCN: Gland.

THE 'SAFETY' OF BIOLOGICAL CONTROL AGENTS: ASSESSING THEIR IMPACT ON BENEFICIAL AND OTHER NON-TARGET HOSTS

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Abstract

Sands, D.P.A., 1997. The 'safety' of biological control agents: assessing their impact on beneficial and other non-target hosts. *Memoirs of the Museum of Victoria* 56(2): 611–615.

Biological control agents considered for introduction into Australia must demonstrate a high degree of specificity before approval is given for their release from quarantine. In assessing 'safety', potential agents for weeds are tested to determine if they can damage crops, ornamentals or native plants and for arthropod pests, if they can adversely affect beneficial insects (including biological control agents) or have a detrimental impact on native arthropods. Effective arthropod biological control agents are rarely monospecific in their native range, most being adapted to a group of closely related species of plant or arthropod hosts. When introduced for control of exotic organisms, the potential host range of agents is usually more restricted due to absence or scarcity of taxa closely related to the target. While such agents utilise a target species as preferred host, some potentially valuable agents will on occasions reproduce on non-target taxa including native species. Host preference in agents is difficult to quantify in the confines of a laboratory, a problem more frequently encountered in arthropod than weed programs. Confinement often favours attack on a wider range of organisms than under field conditions and the results of such tests may influence a decision whether to or not, release an organism. In cases where non-target development is demonstrated by narrowly specific agents in quarantine, the benefits of biological control of pests must be weighed against any real detrimental affects to native species. In Australia some agents occasionally develop on non-target taxa but no exotic arthropod agents are known to seriously damage populations of native species. Most threats or extinctions quoted overseas are poorly justified.

Introduction

When introduced for biological control of pests, several predators with broad host ranges (e.g., cane toad, snails) have also detrimentally influenced beneficial and native organisms. They often failed to control the target pests while their impact on non-target organisms has led to some uninformed distrust in biological control programs. The success and environmental benefits from introductions of narrowly specific exotic agents are often overlooked with more public attention given to the impact by generalist predators on native species.

Proposals to import generalist predators into Australia, especially vertebrates, are not now approved. When biological control agents are considered for introduction, tests must confirm a high degree of host specificity before permission is given by relevant authorities for their release from quarantine. In assessing acceptable levels of specificity, potential agents are tested to determine for weeds, if they can damage or reproduce on crops, ornamentals or native plants and for arthropod pests, if they are likely to influence the abundance of beneficial insects

(including other biological control agents), or have an significant impact on native arthropod species. Before release, tests with exotic agents are conducted in quarantine to determine their potential host range and to assess the significance of any development on non-target hosts or prey.

Procedures for testing the specificity of agents for weeds have been widely practiced (Wapshere, 1974) but tests on agents for arthropod pests have not received the same attention (Sands and Papacek, 1993). In most countries other than Australia and New Zealand, host specificity tests are rarely carried out in arthropod programs. For example in the United States agents are only tested if thought likely to attack beneficial organisms (Ertle, 1993). Recently, guidelines (Waterhouse, 1991, Anon, 1995) for conducting biological control projects have included host specificity procedures for testing agents for both weed and arthropod targets. Though there are no known examples for any undesirable impact on beneficial organisms, native flora or fauna by narrowly-specific agents (Waterhouse, 1991), practitioners are focusing

on developing and refining the methods for testing exotic agents with non-target and native invertebrates prior to their release in biological control programs.

Selecting non-target and native species for testing with exotic agents

When selecting non-target and native species for host specificity testing with exotic agents, Wapshire's (1974) centrifugal (phylogenetic) approach is equally valid for weeds and arthropod programs. Both exotic beneficial and native species are selected based on their taxonomic relationships with a target organism. For weeds projects, once plants related to the target are selected, potted plants can be used in host specificity tests. However, there are serious constraints with native arthropods since collecting and maintaining living species for testing with agents may be difficult. The biologies of native arthropods related to a target are frequently unknown, preventing culture of appropriate stages required for tests. Where 100 or more non-target potted plant species are often tested with agents in weeds programs the testing of more than 10 species of non-target arthropods may be impractical and is often unnecessary. Moreover, the anomalies experienced when testing agents in the confinement of cages and insectaries tend to occur more frequently in arthropod than in weed programs (Sands, 1993).

Information on the taxa related to a target species in its native range is most useful when selecting a centrifugal range of species related to a target pest. However, if tribes are not designated it may be difficult to associate genera or species in groups according to their taxonomic relationships. Beneficial organisms related (within the same family) to the target pest should be included when compiling a list of non-target species for host specificity tests. When considered for release, development of a biological control agent on another beneficial agent is generally unacceptable. When testing agents on native species, selected taxa closely related (family, subfamily, tribe or genus) to the target, or in certain cases, those morphologically similar, are often sufficient to provide adequate information on the host specificity of an agent, rather than testing extensive lists of species of distantly-related taxa. Additional species can be included if justified by the initial test series. The methods by which taxa related to an agent select their hosts or prey (e.g., certain taxonomic groups,

pheromones, host size etc.) can be used to guide the design of tests.

Few agents in arthropod biological control programs are monophagous. Most are oligophagous (e.g., develop on other hosts in the same tribe as the target) in their native range. However, they may utilise only the target species or one or two others very closely related to the target, when introduced to a country where the target is a pest.

Some problems with determining host specificity of exotic agents

The methods for determining the host specificity of potential biological control agents for weeds are relatively well established and practiced (e.g., Harley and Forno, 1992; Waterhouse, 1991; Anon, 1995). However, the methods for testing agents for arthropod targets are more varied and are still being developed. These are needed to reflect the different means by which agents locate, oviposit and develop on/in arthropod hosts when compared with agents interacting with plant hosts.

The methods for rearing agents on their host may not be appropriate for host-specificity tests with non-target taxa. Small containers can often be used for agents to induce oviposition, feeding or development in arthropod hosts. However, restricted space often leads to an inaccurate assessment of specificity by disrupting host recognition and acceptance (Sands and Papacek, 1993). When confined, natural enemies of arthropod pests may oviposit on organisms that do not support their development or they may complete development on hosts or prey not attacked in the field. For example, in Papua New Guinea the egg parasitoid, *Ooencyrtus erionotae* Ferrier, is believed to be narrowly-specific to banana skipper, *Erionota thrax* (Linn.), since it has never been reared from other lepidopteran eggs, even when eggs of the related hesperiid, *Cephrenes mosleyi* (Butler) are deposited less than a metre away on palms. However, its host specificity could not be demonstrated accurately in the restricted space of the laboratory since eggs of *C. mosleyi* and other species readily attracted parasitoid oviposition and supported its development (Sands et al., 1991).

Choice tests with a target host and test species caged together may lead to misleading results. Field and Darby (1991) found that the parasitoid, *Sphegophaga vesparum* (Curtis) (Hymenoptera: Ichneumonidae), for biological control of the European wasps, *Vespula ger-*

manica (Fabricius) and *V. vulgaris* (Linnaeus) (Hymenoptera: Vespidae), oviposited in and developed sparingly on two native wasps, *Ropalidia plebeina* Richards and *Polistes humilis* (F.) (Hymenoptera: Vespidae), when exposed in presence of *V. germanica*. However, the parasitoids failed to oviposit when exposed separately to the native species. This attack on non-target hosts may have been stimulated by the close proximity of *V. germanica* providing the necessary kairomones or other ovipositional cues. This and other studies indicate that choice tests with arthropod target and non-target species exposed to an agent at the same time, should be interpreted with caution and led to a recommendation that choice tests are better avoided when alternative methods are available (Sands and Papacek, 1993).

Plant material which is substrate to a host may be required to stimulate host recognition by an agent. Plant kairomones may also influence the behaviour of natural enemies of arthropods and need to be considered when designing the host specificity procedures (Anon, 1995). Olfactometers can sometimes be used to contrast an agents' response to plant volatiles with their response to the host alone. Some cage materials may affect scatter of light entering cages and those made of black materials may be necessary to stimulate mating or oviposition by certain natural enemies of arthropods. Several parasitoids, e.g., some Tachinidae, require sunlight before mating will occur.

Assessing the impact of agents developing on native hosts

Some information is available on native, non-target hosts utilised by exotic agents but very little information is available on their influence on the density of these host populations. For example, the egg parasitoid, *Trissolcus basalis* (Wollaston), contributed to biological control of *N. viridula* in most crops in southern Australia after various imports, the first from Egypt in 1933 (Wilson, 1960). Without parasitisation of *N. viridula* by *T. basalis*, *N. viridula* would undoubtedly be a much more serious pest in Australia. However, this parasitoid is by no means host-specific in Australia where it has been reared from eggs of a range of native Heteroptera, including more than 10 species of Pentatomidae (Waterhouse and Norris, 1987). While alternative hosts for *T. basalis* provide a reservoir for parasitoid in the absence of eggs of *N. viridula* (Waterhouse and Norris, 1987), there

is no evidence in Australia for a decline in the abundance of native species which occasionally act as hosts to this parasitoid (Gross pers. comm.).

Nafus (1993) when studying the natural enemies of the butterflies *Hypolimnys* spp. in Guam, found no detrimental impact by biological control agents even though introduced parasitoids frequently attacked them and one had become the most significant mortality factor for pupae of a native species. For an exotic agent some development on indigenous fauna or flora may be acceptable, provided that the benefit gained by controlling a pest outweighs any slight risks of effects on the abundance of indigenous species. The advantage of an oligophagous natural enemy was described as a 'lying-in-wait' strategy and contrasted with a 'search-and-destroy' strategy of host-specific species (Murdoch et al., 1985). Monophagous agents may sometimes be considered to be at a disadvantage in an exotic range since dispersal between pest infestations can be restricted by a lack of supporting hosts. Every case requires careful assessment based on the results of carefully-planned research.

The following criteria may be useful when assessing acceptable host specificity of an exotic agent for release:

1. Exotic agents are acceptable if narrowly-specific in their native range and shown by tests with related beneficial or native species, to be specific to the target pest in the new environment.
2. If an agent completes development in/on any non-target (beneficial/native) organisms, a decision must be made as to whether this may have any detrimental effects.
3. The ability of a narrowly specific agent to develop in/on non-target organisms should not automatically preclude a recommendation for release.
4. Development in/on some non-target organisms may be acceptable provided the host range has been shown to be narrow (i.e., confined to a small group of organisms related to the target), and provided that the non-target organisms are not preferred to the target.
5. Development in/on some non-target taxa may sometimes be beneficial — when non-target hosts provide a medium for transmission to crop sites (for arthropod pests).

Claims of rarity and extinction induced by exotic agents

Howarth (e.g., 1985, 1991) has suggested that

many extinctions have followed introductions of biological control agents into Hawaii. However, according to Funasaki et al. (1988), only one of 30 biological control agents introduced into Hawaii in the last 15 years has been found to attack native or beneficial species. Cullen (1989) has suggested that when agents are introduced for biological control of weeds, their impact on plants will be limited to very abundant species if the agent is not entirely host specific for the weed and that an agent will not affect those already held in equilibrium by natural enemies, including sparsely distributed or endangered species. The same is likely for arthropod targets.

Biological control of the moth, *Levuana iridescens* Bethune-Baker (Zygaenidae) in Fiji, is often quoted as an example of extinction of a native insect following introduction of an exotic agent. Control of this coconut pest was achieved in 1925 following introduction of the tachinid, *Bessa remota* (Aldrich) (Diptera: Tachinidae), reared from a related Malaysian moth, *Cathartona (Amuria) catoxantha* (Hampson) (Zygaenidae) (Tothill et al., 1930). Howarth (1991) suggested that the last authentic specimen of *L. iridescens* was collected in 1929 (with possible survival of species to 1940s). However, there is a specimen in the Koronivia Research Ministry of Agriculture, Fisheries and Forests Station in Fiji, collected in August 1941.

Paine (1994) reported an outbreak of *L. iridescens* (accompanied by *B. remota*) on coconuts near Vunindawa, Fiji, in 1956. Paine's identification is likely to be accurate since he was familiar with the moth and its parasitoid. He had been associated with Tothill during the biological control program on *L. iridescens*. In view of the rapid control of *L. iridescens*, its rarity by late 1920s and later survival until 1956 (even causing outbreaks), it is probable that *L. iridescens* has not become extinct. Another likely cause for rarity of this moth is change in its original habitat. Coconut plantations have displaced native palms on most of the lowlands in Fiji, leaving little indigenous habitat for the moth to survive on native hosts.

The closely-related *Amuria catoxantha* (Hampson) from which *B. remota* was collected, is extremely rare or absent from coconuts between outbreaks in Java (Kalshoven, 1981). *A. catoxantha* is said to be confined to native palms in rainforest but occasionally causes outbreaks in coconuts when transported by wind (Kalshoven, 1981). These are phenomena quite possible for *L. iridescens* in Fiji. *L. iridescens* was not considered by Tothill et al. (1930), to be native

to Fiji since it behaved in a way similar to an exotic species. *L. iridescens* had almost no native parasitoids prior to the introduction of *B. remota* and after its first appearance in previously unaffected coconut plantations, spread rapidly from Viti Levu towards the eastern, copra-producing islands (Paine, 1994).

As those entomologists reported, most of the zygaenid moths closely-related to *L. iridescens* occur in countries from New Guinea to Malaysia. Though evidence suggests that *L. iridescens* was most likely exotic in Fiji, its presence elsewhere remains unknown — unless Kalshoven's (1981) unlikely claim that *A. catoxantha* and *L. iridescens* are con-specific proves to be correct. Whether or not *L. iridescens* is an exotic species in Fiji, is now extinct, or still survives in rainforest on native palms, this is not an appropriate example of extinction of a native species caused by introduction of an exotic biological control agent. *B. remota* would not now qualify as suitable as a biological control agent since it is not sufficiently specific even to the target family (Zygaenidae) (Waterhouse and Norris, 1987).

Discussion

Improving existing methods and developing techniques for assessing the host specificity of agents in arthropod biological control programs are high priorities for research in Australia. This is especially relevant following recent fears overseas relating to threats of extinction of native invertebrates. A better understanding of the methods by which natural enemies select their hosts is also needed if host specificity tests are to be meaningful. The criteria used to evaluate agents for arthropod pests differ considerably from those used for weeds (Goldson and Phillips, 1990), for example results of host choice tests on agents with arthropods which as shown by Field and Darby (1991), may be misleading. In addition, foraging behaviour of parasitoids is important (Lewis et al., 1990) but is difficult to test in the laboratory.

The range of cues used by each natural enemy to recognise their hosts differ greatly between species. In the past, the influence of plant kairomones has not been considered fully when testing host acceptance by parasitoids. Plants may be important in stimulating host acceptance or rejection by parasitoids. The design and size of cages used for host specificity tests need to be evaluated for each taxonomic group of agents. It may be necessary to ensure that containers are not re-used or ensure that they are free of

residual kairomones or pheromones from a host or its plant substrate before non-target organisms are tested.

Fears that an agent might change its host range and attack other target taxa after introduction are sometimes expressed. However, there are no recorded examples of monophagous or narrowly oligophagous agents changing their host range to cause damage to beneficials, native plants or non-target insects (Waterhouse, 1991). Agents should not be automatically excluded from further consideration when confinement is suspected of causing anomalous results during host specificity testing. When all laboratory tests are inconclusive, it may still be possible to determine accurately the host range of a potentially valuable agent by studies in its native range. In addition, information from the native range may be useful in determining the adaptation of an agent to a particular habitat, e.g., agricultural land and grassland vs rainforest. Very few species are adapted to both environmental situations.

In every example where biological control of a weed or arthropod pest is considered the criteria for safety may sometimes differ, based on the results of host specificity tests, either under quarantine conditions alone or by taking into account information from the agent's indigenous range. There is an urgent need to examine the interaction of exotic agents introduced for past biological control arthropod programs, for example, the development of *T. basalis* on native Heteroptera. Protocols for assessing exotic imports of agents should be developed for arthropods taking account of the often different criteria used in weeds programs.

References

- Anon, 1995. *The FAO code of conduct for the import and release of biological control agents. Draft (3.1.95) technical guidelines*. International Institute of Biological Control.
- Cullen, J.M., 1989. Current problems in host-specificity screening. Pp. 27–36 in: Delfosse, E.S. (ed.), *Proceedings of VII International Symposium on Biological Control of Weeds, 6–11 March 1988, Rome, Italy*.
- Ertle, L.R., 1993. What quarantine does and what the collector needs to know. Pp. 53–65 in: Van Driesche, R.G. and Bellows, T.S. (eds), *Steps in classical arthropod biological control*. Entomological Society of America, Maryland, USA.
- Field, R.P. and Darby, S.M., 1991. Host specificity of the parasitoid, *Sphecopoga vesparum* (Curtus) (Hymenoptera: Ichneumonidae), a potential biological control agent of the social wasps, *Vespa germanica* (Fabricius) and *V. vulgaris* (Linnaeus) (Hymenoptera: Vespidae) in Australia. *New Zealand Journal of Zoology* 18: 193–197.
- Funasaki, G.I., Lai Po-Yung, Nakahara, L.M., Beardsley, J.W. and Ota, A.K., 1988. A review of biological control introductions in Hawaii: 1890 to 1985. *Proceedings of the Hawaiian Entomological Society* 28: 105–160.
- Goldson, S.L. and Phillips, C.B., 1990. Biological control in pasture and lucerne and the requirements for further responsible introduction of entomophagous insects. *Bulletin of the Entomological Society of New Zealand* 10: 63–74.
- Harley, K.L.S. and Forno, I.W., 1992. *Biological control of weeds. A handbook for practitioners and students*. Inkata: Melbourne. 74 pp.
- Howarth, F.G., 1985. Impacts of alien land arthropods and molluscs on native plants and animals in Hawai'i. Pp. 149–179 in: Stone, C.P. and Scott, J.M. (eds), *Hawai'i's terrestrial ecosystems: preservation and management*. University of Hawaii: Honolulu.
- Howarth, F.G., 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* 36: 485–509.
- Kalshoven, L.G.E., 1981. *Pests of crops in Indonesia*. Revised and translated by P.A. Van der Laan and G.H.L. Rothschild. P.T. Ichtiar Baru-Van Hoeese: Jakarta. 701 pp.
- Murdoch, W.W., Chesson, J. and Chesson, P.L., 1985. Biological control in theory and practice. *American Naturalist* 125: 344–366.
- Nafus, D.M., 1993. Movement of introduced biological control agents onto nontarget butterflies, *Hypolympnas* spp. (Lepidoptera: Nymphalidae). *Environmental Entomology* 22: 265–272.
- Lewis, W.J., Vet, L.E.M., Tumlinson, J.H., van Lenteren, J.C. and Papaj, D.R., 1990. Variations in parasitoid foraging behaviour: essential element of a sound biological control theory. *Environmental Entomology* 19: 1183–1193.
- Paine, R.W., 1994. *Recollections of a Pacific entomologist 1925–1966*. Australian Centre for International Agricultural Research: Canberra.
- Sands, D.P.A. and Papacek, D. F., 1993. Specificity requirements for biological control agents. P. 495 in: Corey, S.A., Dall, D.J. and Milne, W.M. (eds), *Pest control and sustainable agriculture*. CSIRO, Division of Entomology: Canberra.
- Sands, D.P.A., 1993. Effects of confinement on parasitoid/host interactions: interpretation and assessment for biological control of arthropod pests. Pp. 196–199 in Corey, S.A., Dall, D.J. and Milne, W.M. (eds), *Pest control and sustainable agriculture*. CSIRO, Division of Entomology: Canberra.
- Sands, D.P.A., Sands, M.C. and Arura, M., 1991. Banana skipper, *Erionota thrax* (L.) (Lepidoptera: Hesperidae) in Papua New Guinea: a new pest in the South Pacific region. *Micronesica Supplement* 3: 95–100.
- Tothill, J.D., Taylor, H.C. and Paine, R.W., 1930. *The*

- coconut moth in Fiji. A history of its control by means of parasites.* Imperial Bureau of Entomology: London.
- Wapshere, A.J., 1974. A strategy for evaluating the safety of organisms for biological weed control. *Annals of Applied Biology* 77: 201–211
- Waterhouse, D.F., 1991. *Guidelines for biological control in the Pacific.* South Pacific Commission: Suva, Fiji. 30 pp.
- Waterhouse, D.F. and Norris, K.R., 1987. *Biological control: Pacific prospects.* Inkata,; Melbourne. 454 pp.
- Wilson, F., 1960. *A review of the biological control of insects and weeds in Australia and Australian New Guinea.* Commonwealth Agricultural Bureau: England. 102 pp.

CONSERVATION OF INVERTEBRATES IN VICTORIA USING THE FLORA AND FAUNA GUARANTEE ACT 1988 — ACHIEVEMENTS AND POTENTIAL FOR IMPROVEMENT.

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Abstract

Reed, J. And Clunie, P., 1997. Conservation of invertebrates in Victoria using the Flora and Fauna Guarantee Act 1988 — achievements and potential for improvement. *Memoirs of the Museum of Victoria* 56(2): 617-622.

Invertebrate conservation in Victoria could be greatly enhanced by changing the way that the *Flora and Fauna Guarantee Act* is used, and also by groups in addition to CNR accepting more responsibility. To date the focus has been largely on single species conservation, an approach which is inefficient and also inadequate for addressing the broader problems of invertebrate conservation. The focus should shift to protection of threatened invertebrate communities and to managing potentially threatening processes, though some protection of single species will still be necessary. However it is also essential that other agencies, academic institutions and so on become more actively involved, for example in research, provision of information for management, and education. CNR lacks the resources to be effective alone.

Background

The *Flora and Fauna Guarantee Act* 1988 can be considered revolutionary legislation. It was the first broadly-based biodiversity conservation Act introduced in Australia. Similar legislation has now been adopted by many other states in Australia, and also by the Commonwealth government. The purpose of the Act is to enable and promote the conservation of flora and fauna, with objectives including to guarantee that taxa can survive, flourish and retain their potential for evolutionary development in the wild, to conserve communities, to manage potentially threatening processes and to ensure that use of flora and fauna by humans is sustainable. A key feature of the Act is that it goes far beyond the protection of single species. It also enables the protection of communities, and tackles the important issue of managing potentially threatening processes. In recognition of the importance of habitat protection, the Act provides a number of mechanisms to facilitate this. As such it provides for a preventative approach.

There are a range of mechanisms to meet the Act's objectives, including the listing process (adding threatened taxa or communities or potentially threatening processes to Schedules of the Act), controls over taking from the wild, the preparation of Action Statements and determination and protection of Critical Habitats.

These are discussed in detail elsewhere (e.g., Butcher et al., 1994; Clunie and Reed, 1995; Mansergh et al., 1995). The ability to delist items is an important aspect of the Act which is worth noting. There are two reasons for delisting. Firstly, improved management can secure a taxon's or community's survival in the wild. This should be recognised as a fundamental and long-term objective for all listed taxa and communities. Secondly, additional research carried out as a result of listing may reveal that the conservation status of an item is different to that previously thought.

Now that the Act has been in operation for over seven years, it is valuable to assess its achievements as well as identify its shortfalls. It is important to assess which areas require improvement and to understand why. Criticism of the Act without worthwhile suggestions for improvement are of little value.

Achievements

Perhaps the most significant achievement has been that invertebrate conservation is now firmly on the conservation agenda. Those working within the Department of Natural Resources and Environment (NRE) as well as the broader community are now more aware of the importance of conserving invertebrates, and impacts of various activities on invertebrates are now given

equal consideration to impacts on more traditionally recognised fauna.

To date, 24 invertebrate taxa and two invertebrate communities have been listed or recommended for listing under the Act. Eleven potentially threatening processes have also been listed, or recommended for listing, at least partially on the basis of posing a threat to invertebrates. Fourteen Action Statements have been published or exist as drafts; these include ten taxa, two communities, and two potentially threatening processes.

The Act requires that public authorities have regard to flora and fauna management objectives. This is reflected in the increased consultation and negotiation both within the Department, and between the Department and other land and water managers over listed taxa, communities or potentially threatening processes. Production of Action Statements involves extensive consultation with land or water managers and also any other members of the community who ask to be involved. This improves the public profile of invertebrates, raises community awareness, and also means that land or water managers take into account the conservation of listed items and appropriate management of processes. Managers who are advised of the presence of a listed taxon or community within their area of operation, or of a potentially threatening process which they may be contributing to, have been generally fairly open to discussions on ways to modify their activities to take into account the protection of items. These include such diverse groups as Shire Councils, the Alpine Resorts Commission, River Management Authorities and CNR Forest Service. Communication within CNR over appropriate management has also improved through the Action Statement process. For example, negotiations with CNR Forest Service regarding the protection of streams where Alpine Stonefly *Thaumatoperla flaveola* occur have resulted in retention of wider streamside buffers than would previously have been the case. The National Parks Service also takes into account the presence of listed items when preparing management plans.

Another significant benefit of listing and of Action Statement preparation has been the attraction of funding, that might previously have been unavailable, for specific actions necessary to protect taxa and communities and manage potentially threatening processes. Funding for research and protective actions for listed invertebrates and communities has come from a

number of bodies including CNR, Australian Nature Conservation Agency, Australian Heritage Commission, Australian Geographic Society and World Wide Fund for Nature. A direct result of this funding has been a significant increase in our knowledge of their distribution and conservation status (e.g., Otway Stonefly, alpine invertebrates, San Remo Marine Community).

There are many examples where listing of items has resulted in direct management action. Two examples are provided below. Protection and management of the San Remo Marine Community has been a direct result of listing and Action Statement preparation. Surveys to identify other occurrences of the community have been undertaken, increasing our sparse knowledge of the marine environment. Recently, the community has been invaded by the exotic grass *Spartina*, posing a serious threat to the community. Introduction and spread of *Spartina* into estuarine environments has received a recommendation for listing as a potentially threatening process. This invasion by *Spartina* is now being controlled. Without listing the community, or recognition of the threatening process, the protection of this area may not have been a management priority.

Another example of the benefits provided by the Act is the management of Butterfly Community No. 1, which occurs at Mt Piper. Following listing, the public profile of the Butterfly Community has greatly increased. Protection of this community has focussed on appropriate planning, management, research and monitoring and has involved extensive liaison between the Department, the local Shire and adjoining landholders. The extensive research is demonstrated by the presentation of a number of related papers at the Invertebrate Biodiversity and Conservation Conference.

A further achievement of the Act has been that two taxa have been recommended for delisting. In these cases, data obtained subsequent to listing has enabled the more accurate determination of the conservation status of these taxa. Prior to the advent of the Act, this information may never have been collected because of the lack of interest and funding into invertebrate conservation. Lack of information is a significant handicap to appropriate management.

The increased awareness of those outside CNR can be demonstrated by the involvement of some academic institutions in the Flora and Fauna Guarantee process. For example, a third year subject within the Melbourne University

Zoology Department requires students to prepare versions of Action Statements. This has enabled a large number of students to become aware of the objectives of the Act and its implementation. Many of these students are likely to continue in science or become land and water managers who will be need to understand the Act. Ongoing contact between CNR staff and students from other institutions indicates that awareness of the *Flora and Fauna Guarantee Act* 1988 is reasonably widespread.

Improvements

It should be recognised that the introduction of the Act has led to an improvement in the approach to invertebrate conservation in Victoria. However, there are three major issues that need to be addressed to improve its effectiveness in invertebrate biodiversity conservation.

From single-species management to management of communities and threats

Firstly, we need to move away from the focus on single-species conservation, which has been one of the main criticisms of the implementation of the Act. Reasons for this focus are that single-species management has been the more traditional approach and so has a greater acceptance, for example by funding bodies. It can also seem more pressing at the time, especially if a specific threat has been identified. In addition, nominations for single species are more common than for communities or threats, and management is directed toward listed items.

There are times when the single-species approach is valid and necessary. When a taxon is under imminent threat of extinction, immediate targeted action may be essential. Management of flagship species, those which have high public appeal, can be used to focus attention and resources. These species can act as 'umbrella' species if their management will confer protection on other taxa in the same area or with similar requirements. Keystone taxa, which have a critical ecological role and whose survival is therefore essential for the survival of other taxa, may also be a priority. Protection of taxa which are taxonomically isolated can also be important in maximising the protection of genetic diversity.

However, with the vast number of invertebrate species, and the generally poor taxonomic, distributional and ecological knowledge of many groups, this approach is clearly inadequate for dealing with all threatened, or presumed threatened, taxa. It can also be an inef-

ficient use of resources. Tackling the issues related to a single species may result in a narrow approach, while slightly more effort may greatly increase the overall biodiversity benefit. There is also the potential for repetition of effort, where the same issues are dealt with over and over when protecting different species. A broader approach, such as management of a whole community or a potentially threatening process, may avoid this. The problem of single-species preservation has also been recognised in the United States, which established similar legislation over 20 years ago. Bloomgarden (1995) notes that the *Endangered Species Act* 1973 is likely to fail to keep up with the increasing numbers of species needing protection if it continues to focus on single-species protection.

Directing greater effort into nominating and protecting threatened invertebrate communities and managing potentially threatening processes would improve the status of invertebrate conservation.

The benefits of community conservation are that it provides an umbrella effect so that greater biodiversity is protected, it maintains an interactive ecological unit, and, because a community includes undescribed taxa, the problem of poor taxonomic knowledge of invertebrates is avoided. Given the benefits, directing increased attention toward protection of communities is warranted. The identification of threatened invertebrate communities is undisputedly difficult with many scientists disagreeing as to what constitutes a valid community. To date, only two listed communities have been described on the basis of the invertebrate fauna, these are the San Remo Marine Community and Butterfly Community No. 1, which occurs on Mt Piper. Action Statements have been produced for both, and the ongoing management appears to be successful. Most other communities listed have been described on the basis of floristics. An important point is that all components of a community are protected when they are part of that community. Therefore a community need not be described on the basis of the invertebrates in order to provide protection to them.

The identification and management of potentially threatening processes is without doubt the most effective means of conserving invertebrates. As threats are generally broadscale, their successful management can protect a broad range of biota and their habitats. In addition, the nomination and listing of threats draws attention to them within the general community,

which assists in the necessary acceptance of the need for change.

To date, a number of potentially threatening processes have been listed, particularly in relation to the freshwater environment. While only eleven were listed (or recommended for listing) largely or partially on the basis of threats posed to invertebrates, the management of most would assist with invertebrate conservation. For a number of reasons, progress towards producing Action Statements and managing threats has been slower than for single species. Production of Action Statements requires considerably more time, due both to determining appropriate management needs, and also the consultation required to facilitate acceptance by other land and water managers and the community. For changes to be implemented, all those involved, from high level managers to those workers on the ground, must be involved in consultation and be committed to change. The limited availability of people to perform this work, especially as Government departments shed staff, is an obvious constraint.

In most cases, progress toward amelioration of potentially threatening processes can be expected to be slow, and may not be immediately obvious. Frequently, the magnitude of required change is large, and may involve change in entrenched management practices, existing infrastructure, and public opinion. The area over which a threat operates is generally large, and a broad range of stakeholders are often involved, for example Government Departments, River Management Authorities, Shire Councils and individual landholders. Land and water managers may have entirely opposite needs and ideas of managing land to that required for conservation.

With the magnitude of change required, it is not feasible to expect the *Flora and Fauna Guarantee Act* 1988 alone to resolve complex issues and enable all the necessary changes to be implemented. The answer lies more in improving linkages with other programs, policies and legislation, in increasing the level of involvement in new and existing processes and programs with the objective of influencing these to improve management of threatening processes and protect flora and fauna values. Examples are involvement in the Landcare program to reduce sedimentation of streams (which is a potentially threatening process listed under the Act), and input to the Bulk Water Entitlement process in relation to the 'alterations to flow regimes of rivers and streams' also listed under the Act.

Through the Bulk Water Entitlement process there is the potential to allocate appropriate environmental flows to waterways. Consultation between CNR and other land and water managers over threatening processes is ongoing, and is leading to slow changes. For example, CNR maintains a constant involvement with River Management Authorities over the issue of removal of wood debris from rivers, a listed potentially threatening process.

In management of threatening processes, sparse information regarding the ecological requirements of most invertebrates is also a problem — in many cases the precise way in which a threat operates on invertebrates is not known, meaning that appropriate changes in management cannot be identified with certainty.

There is a strong need for education and effective liaison to assist the community to understand why potentially threatening processes detrimentally affect flora and fauna and their habitat, how they can change their current practices and their responsibilities under the Act. Assisting land managers to understand the range of benefits of responsible management to not only flora and fauna and their habitat, but also to their own livelihood in terms of land degradation is an important issue.

Potentially threatening processes are for the most part extremely difficult to manage, and the prospect of resolving inappropriate management is daunting. However, the obvious benefits of management of threats mean that increased effort in this area is justified.

Prioritisation for management

A criticism of the Act has been that invertebrate taxa which we know little about are nominated and listed based on current available information which is often sparse. The nomination process is an open one, and anyone can nominate an item that they believe worthy of listing. Items are nominated for different reasons; they may be clearly threatened, subject to an imminent threat, declining in abundance or distribution, or they may be very rare. It should be recognised that the SAC (the expert panel which assesses the validity of nominations) must make a decision based on available information, and items can only be rejected for listing if they are invalid or ineligible. This approach to decision making is in line with the precautionary principle, which states that 'where there are threats of serious or irreversible environmental dam-

age, lack of scientific certainty should not be used as a reason for postponing measures to prevent environmental degradation' (IAE, 1992). Subsequent surveys may then discover that an item is not in fact threatened, in which case the item is nominated for delisting. This highlights the problem of lack of base line information. However, it is difficult to deny that there are benefits in collecting new information on invertebrates. The issue of poor baseline data has been illustrated by Doeg (this issue), which discusses difficulties in assessing the conservation status of invertebrate taxa.

Rather than condemning the process, the answer lies in adopting a more responsible and methodical approach to management. Without wishing to inhibit public involvement in nominations, it is also necessary for those with access to scientific data and information and/or those with an understanding of ecological processes to ensure that items which are of a high conservation priority are nominated for listing. As listing immediately sets in train a management process, and resources are directed towards listed items, it is critical priority items are nominated. It is inevitable that there will be some prioritisation of management effort because of funding and time constraints. Therefore it is important to ensure that those items given priority are ones which will maximise invertebrate conservation. Appropriate methods should be developed to facilitate prioritisation of management — not only taxa, but also communities and potentially threatening processes. There is an abundant literature available on subject of prioritisation for conservation (e.g., Crozier, 1992; Given and Norton, 1993; New, 1987; Vane-Wright et al., 1991).

Spreading the load

The third area where there is substantial room for improvement lies in groups outside CNR taking on responsibility and ownership of the *Flora and Fauna Guarantee Act 1988*. Rather than viewing the Act as a dry piece of legislation that is the government's responsibility to administer, it should really be viewed as a community-based approach to conservation. Those interested in invertebrate conservation should look more closely at how they can participate in the *Flora and Fauna Guarantee* program to improve its effectiveness. This can only come about through a better understanding of the Act and a willingness to take responsibility. To date, there has been limited involvement by scientists

and the public. For example, a breakdown of those who nominate items for listing demonstrates the involvement of different groups: nominations by CNR represent 46.6% of all received, 33.5% by conservation groups, 15.8% by individuals and only 4% by academic institutions. The low level of involvement with the Act by organisations which are specifically involved in conservation programs means that they do not make use of its benefits for invertebrate conservation. Clearly a broader use of the Act would make it more effective and accepted within the wider community. The lack of involvement to date may be due to insufficient effort in publicising the Act since its establishment or in a lack of responsibility of those outside CNR.

There are a number of areas where the community, including scientists from academic and other institutions, could increase their level of involvement by playing a key role in:

- setting priorities for management of items;
- identifying and nominating threatened communities, and potentially threatening processes;
- providing information and advice for appropriate management of threatened taxa, communities and potentially threatening processes;
- preparation of Action Statements (this would increase ownership and strengthen links between different land management organisations, as well as research institutions);
- increasing advocacy for invertebrate conservation, either as individuals or through organised groups; and
- increasing public knowledge of the *Flora and Fauna Guarantee Act 1988*, for example through school or university courses.

Summary — what we need to do

The advent of the *Flora and Fauna Guarantee Act 1988* has led to a significant improvement in invertebrate conservation in Victoria. Benefits include incorporating consideration of invertebrate conservation in planning and management, increased funding and research and increased public profile. While it has clearly been a step forward, there are ways in which the Act's effectiveness can be improved. Recognising areas which need improvement should lead to further advances in invertebrate biodiversity conservation. A greater focus is needed on the broader approach of management of communities and potentially threatening processes and

setting priorities for nominations and for the management of listed items. Publicising the Act to a greater degree and educating the public on how they can be involved, the effectiveness of the legislation could be significantly enhanced.

References

- Bloomgarden, C. A., 1995. Protecting endangered species under future climate change: From single-species preservation to an anticipatory policy approach. *Environmental Management* 19(5): 641–638.
- Butcher, R. J., Clunie, P. E. and Yen, A. L., 1994. The Victorian Flora and Fauna Guarantee Act: Flagship legislation for invertebrate conservation. *Memoirs of the Queensland Museum* 36(1): 13–20.
- Clunie, P. and Reed, J., 1995. Protection of invertebrates in Victoria: The Flora and Fauna Guarantee Act 1988. *Victorian Naturalist* 112(1): 32–35.
- Crozier, R. H., 1992. Genetic diversity and the agony of choice. *Biological Conservation* 61: 11–15.
- Given, D. and Norton, D., 1993. A multivariate approach to assessing threat and for priority setting in threatened species conservation. *Biological Conservation* 64: 57–66.
- IAE, 1992. Intergovernment Agreement on the Environment.
- Mansergh, I., Jelinek, A. and Clunie, P., 1995. A review of the Action Statement process under the Victorian Flora and Fauna Guarantee Act 1988. Chapter 10 in: Bennett, A., Backhouse, G. and Clark, T. (eds), *People and nature conservation — perspectives on private land use and endangered species recovery*. Surrey Beatty and Sons: NSW.
- New, T.R., 1987. Insect conservation in Australia: towards rational ecological priorities. In: Majer, J. (ed), *The role of invertebrates in conservation and ecological survey*. Western Australian Department of Conservation and Land Management Report.
- Vane-Wright, R.I., Humphries, C.J., and Williams, P.H., 1991. What to protect? — systematics and the agony of choice. *Biological Conservation* 55: 235–254.

ANIMALS ON THE EDGE: THE 'CANCELLING-OUT EFFECT'

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Abstract

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An examination of ground-frequenting invertebrates of forest edges in Tarra-Bulga National Park identified a 'cancelling-out effect' of animals at the order level. Some species increased in abundance towards an edge and other species decreased in abundance at the same edge. Such individual species responses are masked by analysis at the order level. This phenomenon stresses the need for documentation of responses at the species level for a more precise understanding of the effects of habitat edges on distribution patterns of invertebrates.

Introduction

Edge effects along a walking track at Tarra-Bulga National Park in Gippsland, Victoria were examined. The greater variety and density of organisms in the boundary zone between ecosystems has been used to recognise edges (Laurence, 1991). It has been documented by Noss (1991) that abiotic factors play an important role within these transitional zones between edges. Edge effects are described here as the responses of each species to the changed abiotic conditions found at edges.

If species do respond to edges these responses are due to changes in individual microhabitats. Matlack (1993) detected significant differences in abiotic factors including light, temperature, humidity, litter moisture and vapour pressure between the edge interface and the interior of forests. Studies by Bradshaw (1992) indicated that leaf drop, shrub cover and the number of disturbance adapted plants increased within the edge zone of forests.

Recent studies of the effects of edges have revealed that there is not a 'typical' edge response of organisms to edge zones. Sisk and Margules (1993) proposed six hypothetical edge responses which can be seen in Figure 1. Figure 1a illustrates a habitat generalist, where there is no significant change in abundance due to the ability of this species to utilize both habitats and the edge zone equally. Figure 1b depicts a habitat specialist. These species can only exploit one habitat and decline rapidly in abundance at the edge zone of the unsuitable habitat. Figure 1c represents a habitat generalist edge exploiter. These species have the ability to exploit both habitats and demonstrate an increase in abundance at the edge zone. Figure 1d illustrates a

habitat specialist edge exploiter, being found in one habitat, but increasing in abundance at the edge zone before exhibiting a very rapid decline. Figure 1e represents a habitat generalist edge avoider, where these species occurring in both habitats and demonstrating declines in the edge regions where they are unable to exploit the environment successfully. Lastly, Figure 1f is an example of a habitat specialist edge avoider. These species occur in only one habitat and show a decreased abundance as they approach the edge zone. Sisk (1992) was able to recognise these six edge responses in bird communities in California.

During the study of edge effects at Tarra-Bulga, what we term a 'cancelling-out effect' occurs when analysis is carried out at the order level. This cancelling-out effect can be observed when two co-occurring species show opposite edge responses. Our results suggest that at the order level, abundance does not appear to change at an edge. However, individual species can show dramatic changes in abundance. A number of different edge responses were observed by morphospecies within the four study groups targeted.

Study site and methods

The study was conducted in Tarra-Bulga National Park, 35 km S of Taralgon, approximately 200 km E of Melbourne. The park is on the south-eastern end of the Strzelecki Ranges and is well known for its significant stands of cool temperate rainforest and its prolific populations of ferns (Campbell, 1987). It consists of 1625 hectares with 14 recognised vegetative communities including heavily modified areas (Ashwell, 1991).

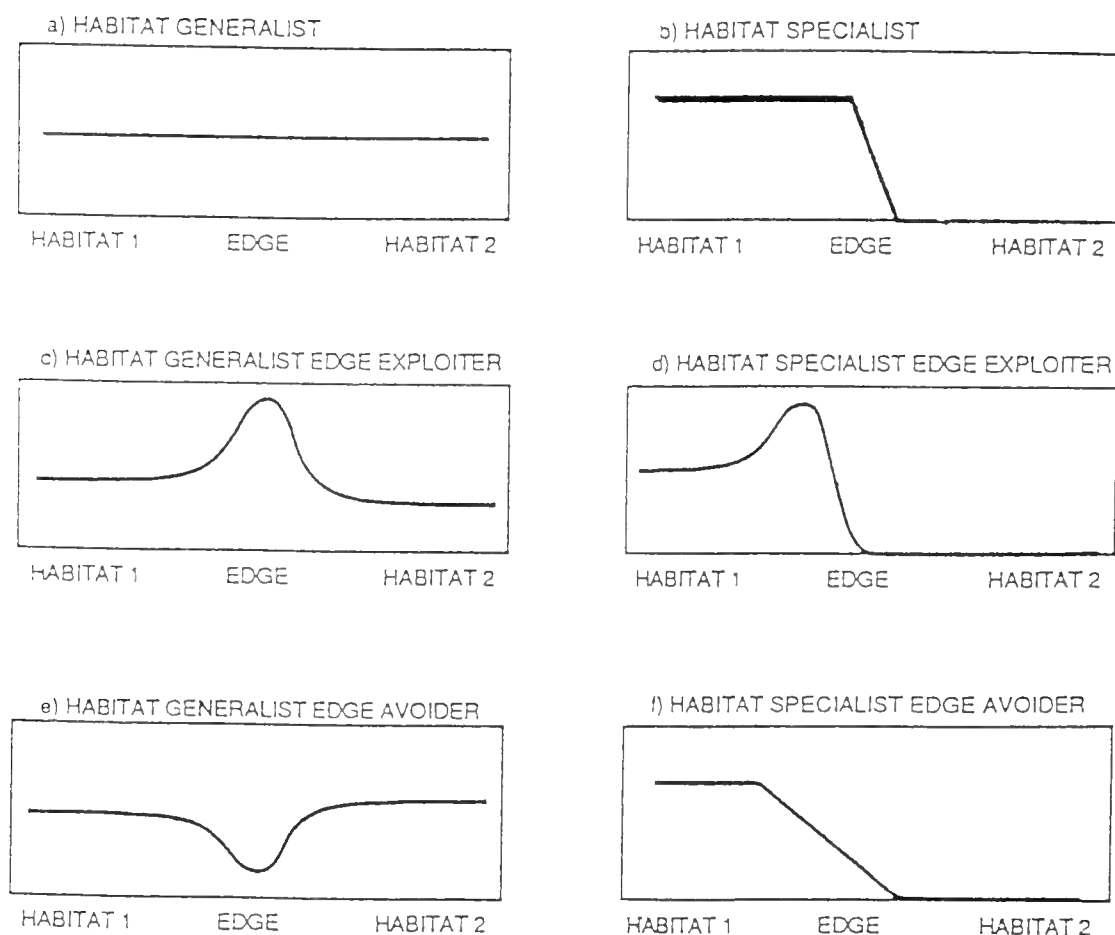


Figure 1. Hypothetical edge responses for species occurring near an abrupt edge between different habitat types (Sisk and Margules, 1993).

Tarra-Bulga National Park in being relatively small could potentially suffer through external forces. A number of roads border and intersect the National Park increasing the edge to interior ratio. A number of walking tracks and fire vehicle access tracks also intersect the park. These areas are in danger of invasion by foreign plant species being carried in by hikers and/or access vehicles. Most roads and walking tracks have the potential to divide habitats and allow altered abiotic factors to modify the composition of edge habitats. The invasion of foreign plant species will enhance this response and may cause dramatic structural differences to these habitats. If edge effects are occurring much of the park may be affected.

Two 88 m transect lines were used as a guide for the sampling of two habitats, wet sclerophyll forest and cool temperate rainforest. Each line straddled a walking track and ran over 40 m into each habitat type. Sampling occurred every 8 m along the transect with five pitfall traps placed to the east of the transect running parallel to the walking track. Soil and litter samples were collected to the west of the transect line at each sampling site. Three sampling techniques were performed in an attempt to reduce the possibility of not sampling all patches within the habitats, and transects were replicated.

All invertebrates were identified to order using Naumann (1991), Harvey and Yen (1993) and Goode (1987). Four detailed studies were

carried out on the orders Araneae, Hymenoptera and Coleoptera and on the Class Collembola. The Araneae were identified to family using Davies (1986) and then to morphospecies. The Collembola and Coleoptera were both identified to family using Naumann (1991) and then to individual morphospecies. Lastly, the Formicidae were identified to genus using Andersen (1991) and Holldobler and Wilson (1990) before being split into morphospecies. The voucher collection has been lodged in the School of Zoology at La Trobe University. Preliminary statistical analysis has been carried out using chi-squared analysis in order to identify edge responses. No statistical results are reported here, but some edge responses are signified. Error bars have not been included on graphs for the sake of simplicity.

Results and discussion

In presenting the results, a hypothetical example is first given to illustrate the cancelling-out effect. Figure 2 shows the abundance of hypothetical species A. It can be observed that this species is a habitat A specialist edge avoider, occurring in large numbers within the interior of habitat A and decreasing in abundance towards the edge zone. Hypothetical species B is depicted in Figure 2B. This species is a habitat B specialist edge avoider (occurring in high abundances within habitat B and decreasing towards the edge zone). At the species level, these two responses are clear. However, at the order level (Figure 2C) it can be observed that there appears to be relatively equal level of abundance across all sites along the transect. It seems that there is a single edge response, that of a habitat generalist.

The actual trends observed were not this clear. Figure 3 represents the total abundance of 19 collembolan morphospecies over one of the transects. Sites A to C represent the wet sclerophyll forest with site A being the most interior site and C being the site closest to the edge zone. Sites D to F represent the cool temperate rainforest with D being the site closest to the edge and F being the most internal site. The symbol WT represents the walking track or edge zone over which the transect straddled. It can be observed from this figure that there seems to be little if any edge effect present. The only trend observed is that of the habitat generalist, where the species present are able to exploit both habitats and the edge zone successfully. Values of

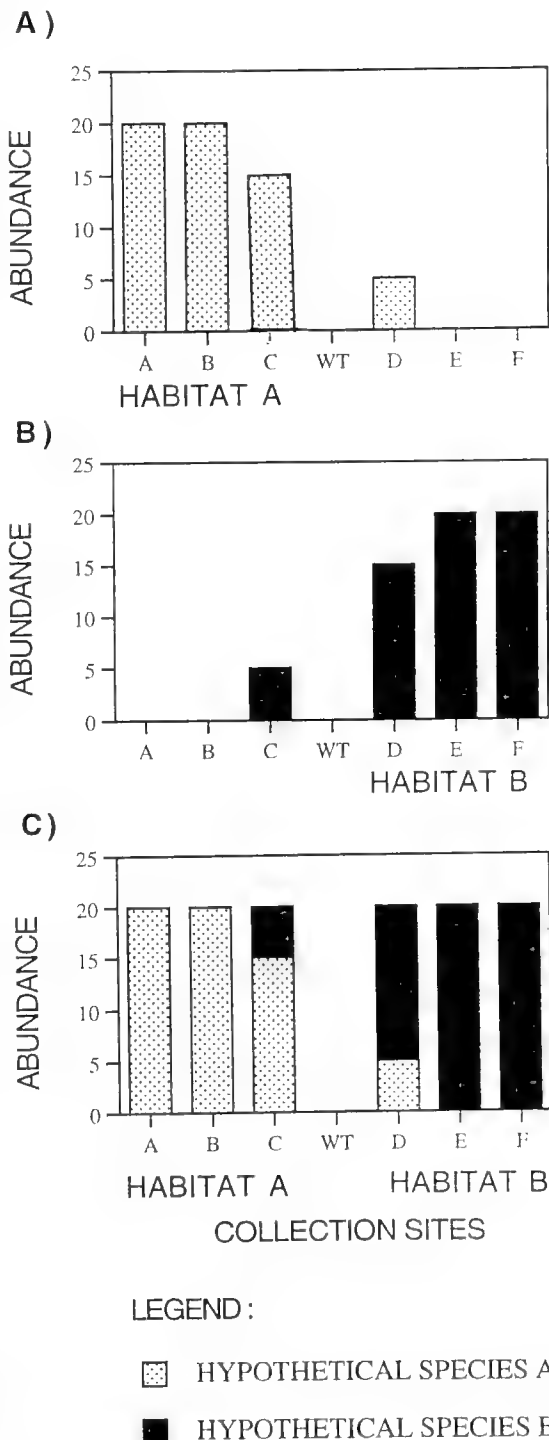


Figure 2. A hypothetical example of the 'cancelling-out' effect where A and B represent hypothetical species and C represents the total abundance of hypothetical species A and B (WT = walking track or edge zone).

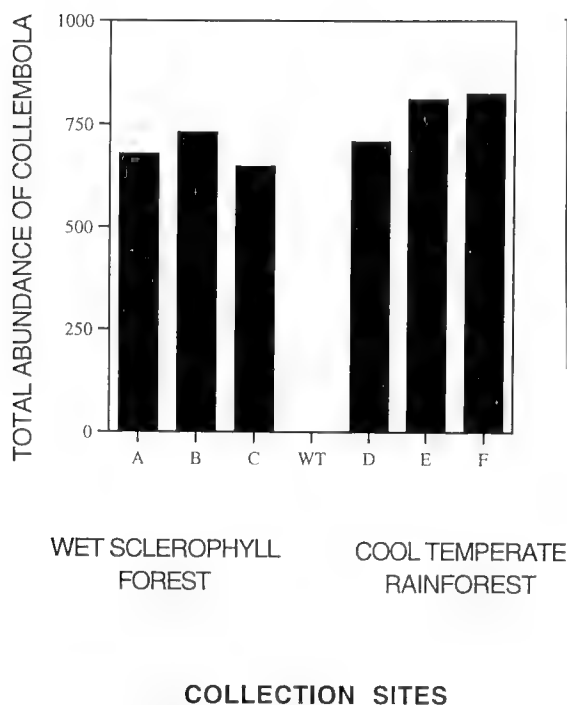
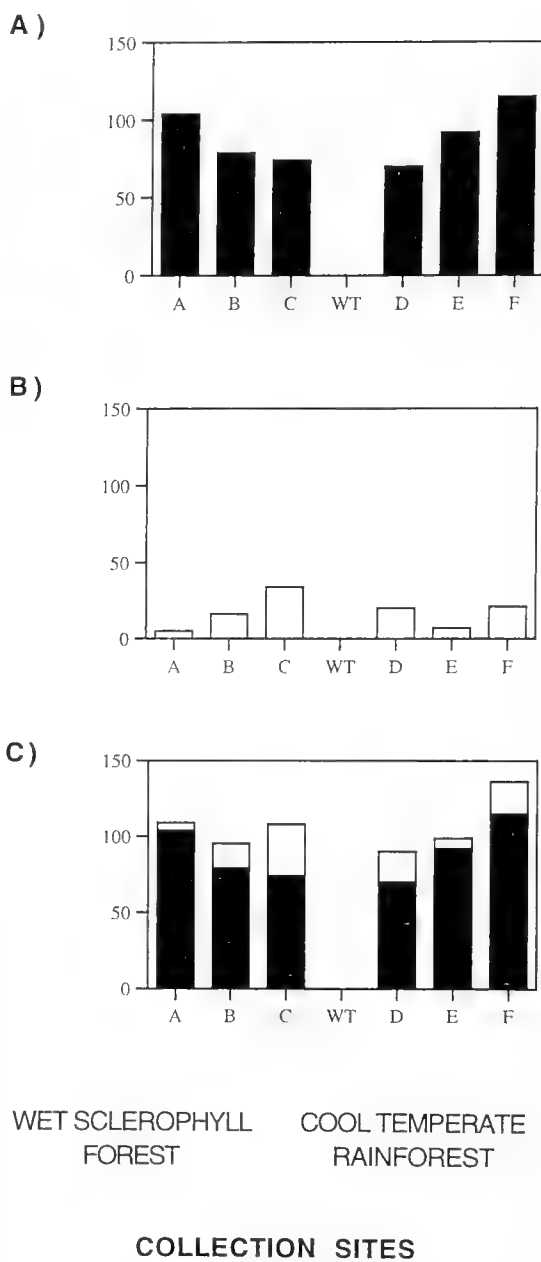


Figure 3. Total abundance of 19 collembolan morphospecies over the transect (WT = walking track or edge zone).

abundance seem to remain relatively constant over the entire transect.

However, when we look at individual species, for example, a species from the family Brachystomellidae and a species of Entomobryidae we can observe two individual trends. Brachystomellidae morphospecies 1 tends to decrease over the transect towards the edge zone suggesting a habitat generalist edge avoider (Figure 4A). Entomobryidae morphospecies 1 (Figure 4B) demonstrates the opposite trend in wet sclerophyll forest, and a mixed response in cool temperate rainforest. When these two species abundances are plotted together (Figure 4C) it can be observed that these two species responses can no longer be distinguished. The trends in the wet sclerophyll forest are lost and it can be assumed that these species are wet sclerophyll forest generalists with no response to the edge zone. This additive response is very similar to that found for the total collembolan abundance histogram (Figure 3).

The cancelling-out effect can also be observed within the order Coleoptera. Figure 5 presents the total abundance data for the 116 coleopterian morphospecies at each site over the entire tran-



LEGEND:

- BRACHYSTOMELLIDAE MORPHOSPECIES 1
- ENTOMOBRYIDAE MORPHOSPECIES 1

Figure 4. Abundance of Collembola. A, Brachystomellidae morphospecies 1; B, Entomobryidae morphospecies 1; and C, Brachystomellidae morphospecies 1 and Entomobryidae morphospecies 1 (WT = walking track or edge zone).

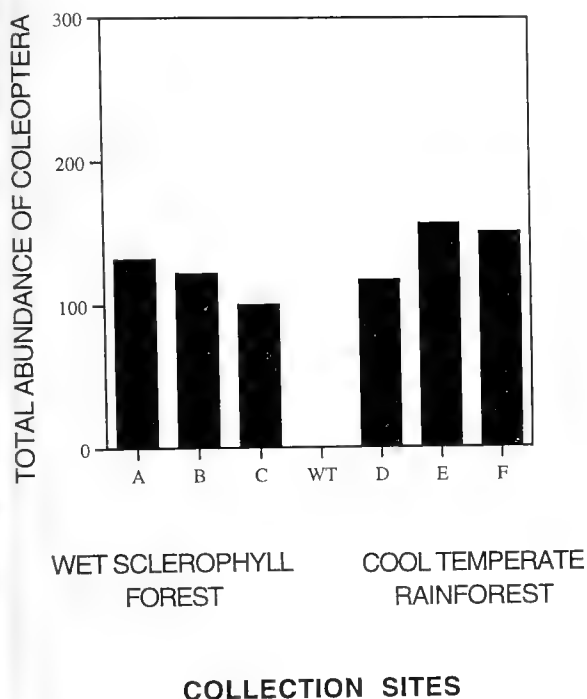
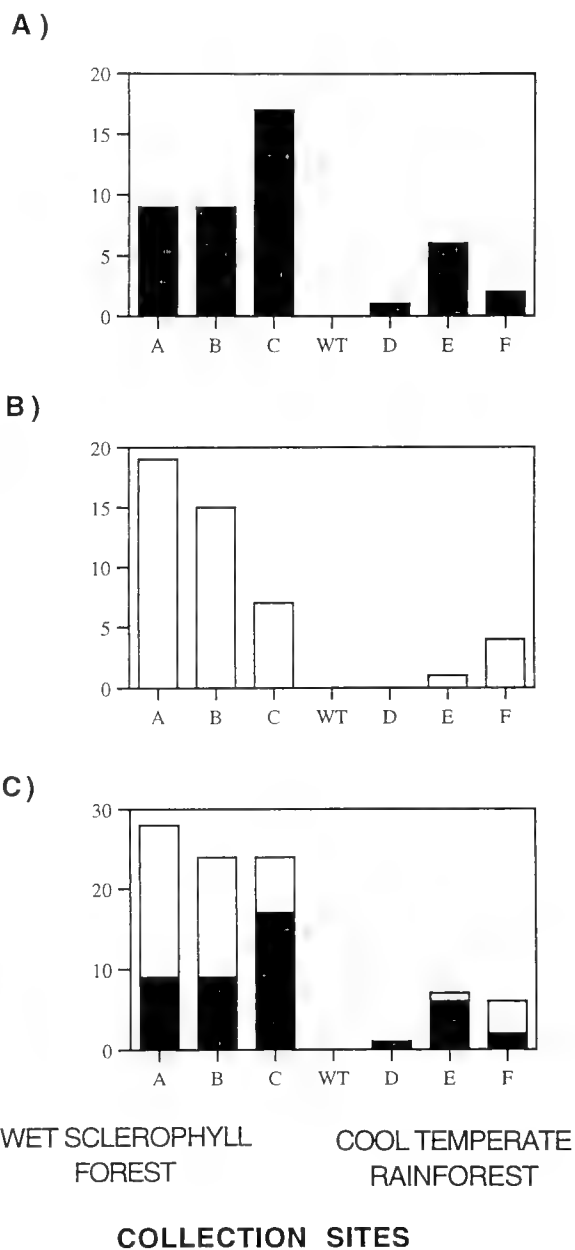


Figure 5. Total abundance of 116 coleopteran morphospecies over a transect (WT = walking track or edge zone).

sect. It appears from this figure that this order is composed of species which are habitat generalists. There seems to be no clear edge effect. However, when these data are examined at the morphospecies level, edge trends can be observed. For example, Curculionidae morphospecies 1 could be classified as a wet sclerophyll habitat specialist edge exploiter (Figure 6A). It can be observed that there are higher abundances of this morphospecies within this habitat and an increase in abundance at the edge zone. However, Curculionidae morphospecies 2 demonstrates a different trend (Figure 6B). It is suggested that this morphospecies is a habitat generalist edge avoider, having decreased abundances at the edge zone. When these two morphospecies from the same family are plotted together, a very different trend can be observed. Abundances become more similar between sites within each habitat. The family level analysis leads to a cancelling-out of species trends, masking how individual species are responding to edges.

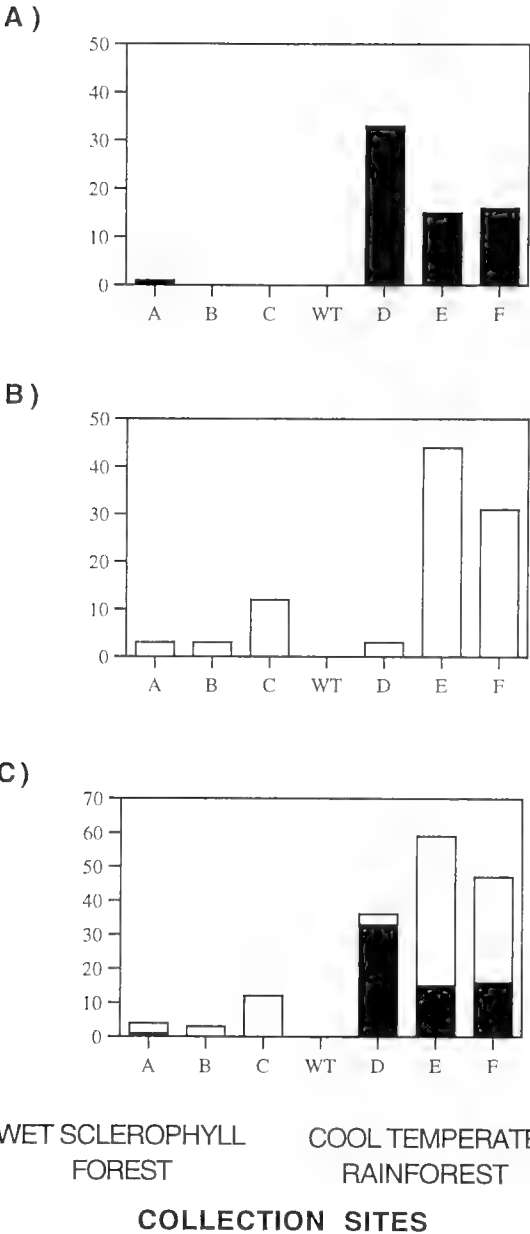
Another beetle example shows this cancelling-out effect a little less clearly. Staphylinidae morphospecies 1 is a cool temperate rainforest specialist edge exploiter (Figure 7A). Leiodidae



LEGEND:

- CURCULIONIDAE MORPHOSPECIES 1
- CURCULIONIDAE MORPHOSPECIES 2

Figure 6. Abundance of Coleoptera. A, Curculionidae morphospecies 1; B, Curculionidae morphospecies 2; and C, both morphospecies of Curculionidae (WT = walking track or edge zone).



LEGEND:

- STAPHYLINIDAE MORPHOSPECIES 1
- LEIODIDAE MORPHOSPECIES 1

Figure 7. Abundance of Coleoptera. A, Staphylinidae morphospecies 1; B, Leiodidae morphospecies 1; and C, both Staphylinidae morphospecies 1 and Leiodidae morphospecies 1 (WT = walking track or edge zone).

morphospecies 1 could be classified as a cool temperate rainforest specialist showing dramatic decreases in wet sclerophyll forest and at the edge of the rainforest (Figure 7B). However, when these two species from different families are plotted together (Figure 7C) it can be observed that the differences in abundance between adjacent sites decreases. Once again, by simply adding the abundances for two species together, the individual trends observed at the species level are slightly cancelled out.

Although this cancelling-out effect has been observed within the Collembola and Coleoptera, the Formicidae remain variable in abundance over the transect (Figure 8). The cancelling-out effect does not seem to apply for ants in this study. A number of factors may explain this. It has been demonstrated by numerous researchers that particular groups of species prefer particular environmental conditions. The most abundant ant at these sites was a species of *Notoncus* which are generally known to prefer wetter sites, being cool-adapted species and are often nocturnal foragers (Andersen, 1986). They are often competing directly against *Iridomyrmex* species and it is believed that this has caused the nocturnal habit to evolve. The second most

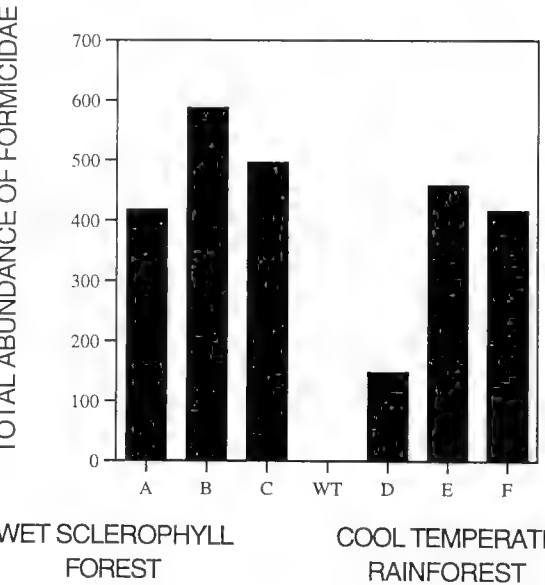


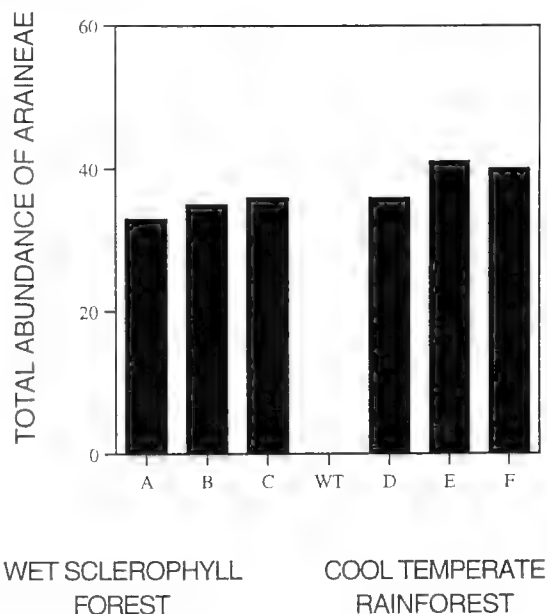
Figure 8. Total abundance of 12 morphospecies of Formicidae (Hymenoptera) over a transect (WT = walking track or edge zone).

common ant species was a species of *Monomorium*, which are known to prefer open habitats. Due to the unspecialised behaviour of many species of *Monomorium* they are very successful opportunists (Andersen, 1984). The third most common species belongs to the genus *Iridomyrmex*, of functional group one, or the dominant group. These species are abundant, aggressive and are known to monopolise resources (Andersen, 1984). They also prefer sunny, open conditions. Competitive interactions between ants has led to the development of tightly structured communities in the arid zone (Greenslade, 1979) and may be partly responsible for the variation observed over the transect. The ability of ants to forage over large distances will also play a role in the variation of abundance over the transect. Due to these high levels of mobility, the association between the organisms and a particular microhabitat will be reduced. Therefore, particular ant species will be found in more sites along the transect due to their ability to forage over large areas. For ants social interactions may also play a large role in the variable distribution observed along the transects.

One other order of arthropods were examined, the Araneae. As for the Collembola and Coleoptera, spiders demonstrate similar abundances across all sites along the transects at the order level (Figure 9). Once again, the only trend observed at the order level is that of the habitat generalist.

However, when examining the spider data at the morphospecies level a number of trends can be observed. Figure 10A depicts the abundance of Cycloctenidae morphospecies 1. This species is declining towards the edge in wet sclerophyll habitat and declining towards the interior of the cool temperate rainforest. The abundance of Cycloctenidae morphospecies 2 can be observed in Figure 10B. This morphospecies represents an increase within the middle sites of the wet sclerophyll habitat and increases towards the interior of the cool temperate rainforest. Figure 10C includes the abundance of both morphospecies of Cycloctenidae. The trend within this family changes to that of the habitat generalist for the cool temperate rainforest.

Other factors play a role in the cancelling-out effect. Sampling bias, and the difficulty in providing a sampling regime that will account for patchiness within the environment is also important. Three sampling techniques were performed during this study in an attempt to reduce the possibility of not sampling all patches within the habitats, and transects were replicated.



COLLECTION SITES

Figure 9. Total abundance of 31 morphospecies of Araneae over a transect (WT = walking track or edge zone).

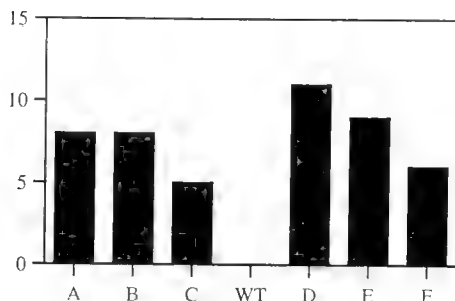
Generalist trends may appear at the family and order levels through the combination of inadequate sampling procedures, chance variation and real life differences in individual responses. Without statistical analysis it is not possible to say if the edge responses observed are real. However, preliminary tests using chi-squared analysis indicate significant trends for some species. These trends are lost if analysis is carried out above species level.

It has been demonstrated that a cancelling-out effect occurs at both the family and order level of analysis. To observe trends in ecological systems examining such factors as edge effects it is essential that classification of organisms must be completed to the species or morphospecies level. Only when this has been done will real edge responses be identified. The cancelling-out effect discussed here may have wider implications for ecological studies involving analysis of colonisation trends of organisms after more widespread disturbances such as fire.

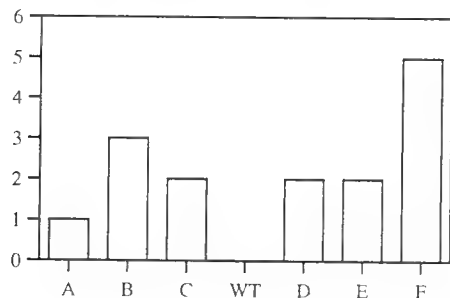
Acknowledgements

Thanks to the Museum of Victoria for providing partial funding for the project through an honours grant. The authors also thank the

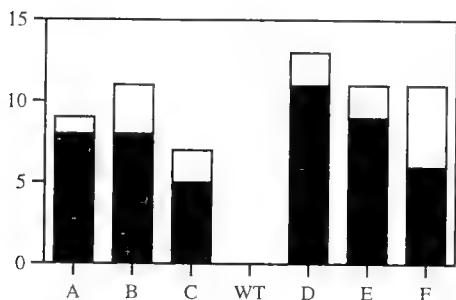
A)



B)



C)

WET SCLEROPHYLL
FORESTCOOL TEMPERATE
RAINFOREST

COLLECTION SITES

LEGEND:



CYCLOCTENIDAE MORPHOSPECIES 1



CYCLOCTENIDAE MORPHOSPECIES 2

Figure 10. Abundance of Araneae. A, Cycloctenidae morphospecies 1; B, Cycloctenidae morphospecies 2; and C, both Cycloctenidae morphospecies 1 and 2 (WT = walking track or edge zone).

anonymous reviewer for helpful comments on the manuscript.

References

- Andersen A.N., 1984. Community organization of ants in the Victorian Mallee. *Victorian Naturalist* 101(6): 248–251.
- Andersen, A.N., 1986. Patterns of ant community organization in mesic southeastern Australia. *Australian Journal of Ecology* 11: 87–97.
- Andersen, A.N., 1991. *The ants of southern Australia — a guide to the Bassian fauna.* CSIRO: Melbourne.
- Ashwell, D.A., 1991. A vegetation survey of Tarra-Bulga National Park, Victoria. *Arthur Rylah Institute for Environmental Research, Technical Report Series* 105.
- Bradshaw, F.J., 1992. Quantifying edge effect and patch size for multiple-use silviculture — a discussion paper. *Forest Ecology and Management* 48: 249–264.
- Campbell, R., 1987. *National Parks of Victoria, South Australia and Tasmania.* Reader's Digest Services: Surrey Hills.
- Davies, V.T., 1986. *Australian spiders (Araneae) — collection, preservation and identification.* Queensland Museum Booklet 14, Brisbane.
- Goode, J., 1987. *Insects of Australia.* Angus and Robertson: North Ryde.
- Harvey, M.S. and Yen, A.L., 1993. *Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates.* Oxford University Press: Melbourne.
- Holldobler, B. and Wilson, E.O., 1990. *The ants.* Harvard University Press: Cambridge.
- Greenslade, P.J.M., 1979. *A guide to ants of South Australia.* South Australian Museum: Adelaide.
- Laurence, W.F., 1991. Edge effects in tropical forest fragments: applications of a model for the design of nature reserves. *Biological Conservation* 57: 205–219.
- Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66: 185–194.
- Naumann, I.D., 1991. *The insects of Australia — a textbook for students and research workers.* Melbourne University Press: Melbourne.
- Noss, R.F., 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth Florida hammock. *Natural Areas Journal* 11(1): 34–46.
- Sisk, T.D., 1992. *Distribution of birds and butterflies in heterogeneous landscapes.* Ph.D. dissertation, Stanford University: Stanford.
- Sisk, T.D. and Margules, C.R., 1993. Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. Pp. 57–68 in: Saunders, D.A., Hobbs, R.J. and Ehrlich, P.R. (eds), *Nature conservation 3 — the reconstruction of fragmented ecosystems.* Surrey Beatty and Sons: Perth.

A PRELIMINARY ASSESSMENT OF ANANGU KNOWLEDGE OF CENTRAL AUSTRALIAN INVERTEBRATES

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Abstract

Yen, A.L., Gillen, J., Gillespie, R., Vanderwal, R. and the Mutitjulu Community, 1997. A preliminary assessment of Anangu knowledge of Central Australian invertebrates. *Memoirs of the Museum of Victoria* 56(2): 631-634.

There is a growing recognition that the knowledge of indigenous peoples can be invaluable in ecological studies and environmental management. While there is now an expanding literature recording indigenous ecological knowledge, most of it focuses on indigenous knowledge of flora and vertebrate fauna, with only passing references to invertebrate fauna. This has also been true in Central Australia, where important recent studies of Aboriginal ecological knowledge have focussed on the relationships between vertebrates and flora. There is only fragmented information on Aboriginal knowledge of invertebrates in Central Australia, primarily the use of invertebrates as a food source and linguistic studies that record invertebrate names. A project was initiated with Anangu from the Mutitjulu Community at the Uluru-Kata Tjuta National Park, who speak Pitjantjatjara, to learn about their names for invertebrates, their knowledge on the biology of invertebrates, and their possible use of invertebrates as environmental indicators. The methods adopted in this project are outlined and some preliminary results presented.

Introduction

The existing literature on Aboriginal knowledge of invertebrates suggests that it is restricted to those that are of economic value and to a few invertebrates that are culturally significant, for example in creation stories. Aboriginal knowledge regarding invertebrates is primarily associated with their use as a food resource, especially witjuti (witchetty) and bardi grubs, honey ants, molluscs and honey bees (Campbell, 1926; McKeown, 1944; Bodenheimer, 1951; Tindale, 1966; Calaby, 1971; Tindale, 1981; Devitt, 1989). Often this information is generalised, using a mixture of information from different parts of Australia from Aboriginal tribes of different language groups, and has been gathered without clear scientific identifications of the invertebrates being named or described. This has resulted in the use of a mixture of confusing common names that have been applied nationally: e.g., bardi and witjuti grubs.

From the point of view of western science, invertebrate diversity and abundance suggests that they are a potentially very powerful group of environmental indicators (New, 1995), and it is important to ascertain whether the hunter-gath-

erer societies of arid Australia also attributed environmental values to invertebrates.

A recently initiated survey of invertebrates at Uluru-Kata Tjuta National Park by the Museum of Victoria provided an opportunity to undertake a collaborative project with the traditional owners to record their knowledge of the invertebrate fauna. The Anangu, the traditional owners of this region of the Western Desert, had already been working with scientists and park managers to record their traditional knowledge of plants and vertebrate fauna as part of the long-term sustainable management of the park (Reid et al., 1992; Baker et al., 1993). The Mutitjulu Community, located within Uluru-Kata Tjuta National Park, agreed to share some of their knowledge of invertebrates with the scientists, with a view to preparing a guide to the invertebrates of the park that would demonstrate this aspect of Anangu knowledge of their land and the ways in which they care for their country.

The primary language of Anangu is Pitjantjatjara, which is the language spoken in part of the Western Desert region of Australia and encompassing the Great Victoria Desert, although the languages in the Simpson and Gibson Deserts

(e.g., Ngaanyatjarra, Ngaatjatjarra, Yankunytjatjara, Luritja and Pintubi) belong to the same language group as Pitjantjatjara (Hobson, 1990). A considerable number of invertebrate names had already been recorded in the Pitjantjatjara/Yankunytjatjara to English Dictionary (Goddard, 1992), based on earlier linguistic studies. The project at Uluru provided an opportunity to check some of the terms previously recorded and to clear up some of the ambiguities and uncertainties in Goddard (1992).

The aims of the project are to record Anangu knowledge in three areas: (1) invertebrate names and their cultural classification; (2) observations on the biology of these invertebrates; and (3) information on the ecology of these invertebrates. This paper will focus primarily on the process involved in documenting Anangu information about invertebrates and only a few preliminary results will be presented.

Methodology

The work was undertaken within the lands of the Mutitjulu Community at Uluru. Data recorded was obtained by:

1. showing specimens (whether dead or alive) to Anangu and recording their responses, and
2. walking around with Anangu in the bush and letting them speak about invertebrates of their choosing.

Records were made on audio tape, notes were taken in cross reference to the tapes, and photographs were taken of all invertebrates examined in this way. The intellectual property rights of the Anangu are protected by recognising that all information provided by them remains the property of the Mutitjulu Community and their permission is required for future use. Furthermore, no information recorded will be made public until the Community verifies accuracy and ownership of the information.

The invertebrate research took place over 8.5-day contact sessions in October 1994 and March 1995, and a full day in October 1995. Anangu participants at each session ranged from two to five, in addition to one to two trainee Aboriginal rangers and an interpreter. The sessions were conducted primarily in Pitjantjatjara, with an interpreter. The information was provided by the following members of the Mutitjulu Community: Trigger Derek, Imjuka (Jenny Watson), Mr Jingo, Mary Kayukayu, Alan Kenda, Kata Kura, Edith Richards, Norman Tjakalyiri, Johnny Tjalyiri, Barbara Tjikatu, Daisey Walkabout, Tommy Wangi, Billy Wara, and Witja-

wara (Rosie Curtis). Assistance was provided by the following trainee rangers: Narelle Tjimpuna Ah Chee, Akana Campbell, Nyinku Jingo, and Peter Wilson (Kunmanara).

There are several constraints in documenting Anangu knowledge, and the issues involved were discussed in more detail by Baker et al. (1993) in relation to their work with Anangu on the vertebrate fauna at Uluru. The constraints include the following.

The Tjukurpa

The Tjukurpa is the 'Law' by which Anangu life is governed. It is information that outlines relationships between all plants and animals, their relationship to the land, and their relationship to human beings (Baker et al., 1993). This means that much of the biological or ecological knowledge about the behaviour and distribution of plants and animals is knowledge of the Tjukurpa. There is a wealth of information in the Tjukurpa, but some is public information and some is restricted information. Restricted information is only available to those adults, who according to traditional Law, have the right to know and manage it. In general, information about identification and description is within the realm of public knowledge (What is it? Where does it live? What does it eat/What eats it?) fall into this category. Questions about relationships and origins may fall into the restricted category (Why is it called this? Why is this the same as? How is this related to that?).

Age, sex and status of informants

While much of the information on the ecology of the land can be obtained from Tjukurpa, some is also accumulated through generations and through personal experience; what Anangu consider to be true is the result of practical personal experience and religious/ceremonial training over their lifetime. Hence older members of the community generally possess greater knowledge than younger members. Some types of knowledge remain in the domain of either male or female members of the community. Hence the amount and level of knowledge that is given may vary considerably depending upon the status of the informants within the community (e.g., deferring to elders; commenting on matters in presence of members of the other sex).

Language

As with all studies involving different languages, there are always the issues involving different dialects, transcribing Pitjantjatjara words into standard phonetically spelt forms,

and filtering information through a non-scientific interpreter. Words can fall from use for some time (months or years) following the death of a person in the community whose name had a similar sound, and another new name will come into use (the Kunmanara factor). It is possible that a particular word will become lost to the language.

Culture

Cultural differences undoubtedly influence the amount of knowledge obtained. Anangu are more willing to give information when working with smaller groups. They do not appreciate aggressive questioning, and the essence of obtaining information is the willingness to spend time with them, to observe, to learn and to respect the knowledge of elders. Our initial approach was based on a fairly standard western scientific one of showing specimens and asking questions, and this often quickly led to boredom. Western scientific classification and principles are irrelevant to Anangu, and they do not view invertebrate information with the cause-effect principles of western science; Anangu are very firm in that the knowledge they possess is certain and correct, often as a result of Tjukurpa.

Results and discussion

Previous studies on plants and vertebrates indicate that the extent of accurate botanical and zoological knowledge possessed by Anangu is formidable. It is based on pragmatic observations. While the known number of invertebrate words is small (relative to the number of different invertebrates), our preliminary work suggests that their knowledge in this area is much greater than previously assumed.

Pitjantjatjara invertebrate names

The first observation about Pitjantjatjara invertebrate names is that there is no general term for invertebrates or insects. To indicate invertebrates as a group, reference is made by listing several of them (e.g., flies, ants, butterflies, spiders, snails, etc).

The Pitjantjatjara/English Dictionary (Goddard, 1992) has the following number of invertebrate words: adult stages (45 names), immature stages (13), insect galls (6), psyllid lerps (1), scale insects (2), silken webs or bag moths (2), termite nests (2), and honey ants (4–6). With the adult names, most correspond to the ordinal level or above. There are three names that are applied to invertebrates from different orders: wanka

(spiders and silk-spinning caterpillars), kawalpa (stick insects and mantids) and mirin-mirinpa (crickets and cicadas). There is a small number of general names for some invertebrate groups such as wanka (spiders), mutu-mutu (beetles), minga (ants) and maku (edible grubs). So far, thirteen names for immature insects are known, and 10 refer to edible grubs belonging to either the Coleoptera (beetles) or Lepidoptera (moths). There are undoubtedly many more Anangu names for invertebrates. In our brief work so far, at least seven previously unknown names have been recorded. Some invertebrates simply do not have a name — and this is clearly stated by Anangu on several occasions when specimens were shown to them.

Patterns of classification approaching a western scientific perspective was as interesting as it was frustrating, knowing that the Anangu basis for naming (and relationships between the taxa) may reside in the Tjukurpa and may never be revealed to science. Some of the more obvious classificatory ingredients include:

1. Shape: e.g., kawalpa (stick insect and mantid);
2. Sound: e.g., mirin-mirinpa (cricket/cicada);
3. Products: e.g., silk production (wanka);
4. Utility value: more invertebrate groups have general names (e.g., ants = minga), but those of greater economic value or ones with nasty bites or stings (e.g., bulldog ants) may have specific names. In the case of honey ants (tjala), there are names for different life history stages, workers and repletes; and
5. Identifiable tracks and traces: while no invertebrate names can be directly attributed to tracks or traces (with the exceptions of galls and lerps), it is possible that those that make characteristic tracks in the sand will be named because of the importance of tracks in the eyes of Anangu.

The closest to a western scientific binomial classification system is the naming of edible grubs. 'Maku' is the generic term for edible grubs, but different types of maku are sometimes indicated by the use of the name of the plant, e.g., maku lunki from *Acacia kempeana* and maku punti from *Cassia*. There are at least two different types of maku from the River Red Gum; those found in the roots are maku ungan-gungu while those in the trunks or branches are maku ilytjaliti or maku palkapiti. At least 24 plant species in central Australia harbour maku (Latz, 1995), so there could be at least 24 different maku names. It is interesting to note that there is no corresponding number of names for

adults of maku. Similarly, for example, adult Lepidoptera were of little interest to the Tzeltal Indians of South America (Hunn, 1982), yet their larvae, which were important as food or as pests of crops, were carefully sorted into 16 terminal folk taxa.

Anangu biological observations

Anangu possess a great knowledge of invertebrate tracks and traces, even of invertebrates that were not of economic value to them. The hunting behaviour of wolf spiders, the web building behaviour of argiopid spiders, the foraging behaviour of centipedes and scorpions are all well known to many Anangu. The builders of various burrows are known, as well as the structure of the burrow systems and location of the animals within the burrows is usually known.

One interesting observation is the Anangu knowledge of different life history stages of invertebrates. The existence of the egg stage is often not acknowledged and live birth is invoked for a large number of invertebrates. There is also a lack of recognition of metamorphosis; small grubs grow into big grubs, and small beetles grow into bigger beetles. The presence of mating pairs of insects (smaller males) is interpreted as the mother transporting the young on her back. This is an area of great confusion, and even the Pitjantjatjara verbs that describe metamorphosis (Goddard, 1992) give conflicting messages such as 'turn into immature moth,' 'burst out of cocoon case and is a young moth' and 'the grub gets bigger and becomes a fully developed grub.'

Anangu certainly possess a greater knowledge on the biology and behaviour of invertebrates of economic use. For example, the larval, worker, replete and empty replete stages of the honey ant have separate names, as well as the entrances and chambers of the nest; there is also the recognition that there is a dominant ant in the colony. In the case of maku such as the witjuti grub, it is acknowledged that the grub turns into a 'moth' or 'butterfly'.

Habitat preferences

While work so far has concentrated on obtaining information on the Pitjantjatjara names and the biology of the named invertebrates, it is apparent that Anangu possess a wealth of information on the habitat preferences. During the discussion sessions with Anangu, reference was made to the occurrence of particular invertebrates in relation to fire. This knowledge is of major importance in learning about the land, but as with western science, we first have to

know what the animal is before we can study it in detail.

Conclusions

Several questions arise from this study in terms of its scientific value. We are making a mistake if we strictly compare indigenous knowledge or folk classification with western taxonomy and systematics. Indigenous knowledge is more akin to excellent field naturalist or field biologist information, and this is entirely to be expected because Anangu have grown up on the land and learn this information as part of their upbringing.

So what is the relationship between Anangu names and the biological classification of western science? Is there a one to one correspondence (and at what level?), or is there under differentiation or over differentiation (are Anangu 'lumpers' or 'splitters?'). The preliminary answer to this question is that Anangu primarily name invertebrates in accordance with their need to do so. Some invertebrates simply do not have names, others have very general names, while those of greater economic value have detailed names for the life history stages. This finding parallels similar studies of indigenous knowledge of invertebrates conducted elsewhere (Meyer-Rochow, 1975; Sillitoe, 1995).

One issue that scientists need to consider is the treatment of information that we consider to be scientifically incorrect. How do you treat names that do not correspond with biologically valid categories? It is important that indigenous knowledge is recorded accurately, and it is up to scientists to determine why some of these indigenous interpretations have arisen. The moral dilemma is whether scientists should see the information transfer as a one way or two way process. In a couple of instances when Anangu were given scientific information, their reactions varied from one of interest (and 'how did you learn to obtain such information?') to derision ('you don't know what you are talking about!').

These observations are preliminary, but indications are that there is a vast area of Anangu knowledge on the invertebrates. As long as differences with Anangu and scientific approaches to invertebrates are recognised, then there is much to be gained from Anangu that could be very important in the long-term sustainable management of the arid Centre. In terms of the learning process, it is important that Anangu teach us in their own way in their own land. A

comment made by a senior man quoted by Baker et al. (1993) provides a succinct summary of the situation:

'I can't properly talk about the country, teach about the country unless I am in it, walking on it, touching it, looking at it.'

Acknowledgements

The authors wish to thank the staff of the Uluru-Kata Tjuta National Park for their assistance, especially Julian Barry. Linda Rive provided interpretation skills at some of the discussion sessions, and Lyn Baker provided valuable advice on protocol. John Broomfield and Caroline Williamson provided invaluable assistance in the field. The Museum acknowledges the assistance of the Australian Nature Conservation Agency, Australian Geographic, Friends of the Museum of Victoria, Gadsden Rheem Packaging, Sarlon Pty Ltd, Stihl Pty Ltd and Viscount Industries.

References

- Baker, L., Woenne-Green, S. And the Mutitjulu Community, 1993. Anangu knowledge of vertebrates and the environment. Pp. 79-32 in: Reid, J.R.W., Kerle, J.A. & Morton, S.R. (eds), *Uluru fauna: the distribution and abundance of vertebrate fauna of Uluru (Ayers Rock-Mount Olga) National Park*, N.T. Australian National Parks and Wildlife Service: Canberra.
- Bodenheimer, F.S., 1951. *Insects As human food*. Dr. W. Junk: The Hague.
- Calaby, J.H., 1971. Man, fauna, and climate in Aboriginal Australia. Pp. 80-93 in: Mulvaney, D.J. and Golson, J. (eds), *Aboriginal man and environment in Australia*. Australian National University Press: Canberra.
- Campbell, T.G., 1926. Insect foods of the Aborigines. *Australian Museum Magazine* 2: 407-410.
- Devitt, J., 1989. Honeyants: a desert delicacy. *Australian Natural History* 22: 588-595.
- Goddard, C., (compiler), 1992. *Pitjantjatjara/Yankunytjatjara to English Dictionary*. Institute for Aboriginal Development: Alice Springs.
- Hobson, J., 1990. *Current distribution of central Australian languages*. Institute for Aboriginal Development: Alice Springs.
- Hunn, E.S., 1982. The utilitarian factor in folk biological classification. *American Anthropologist* 84: 830-847.
- Latz, P., 1995. *Bushfires & bushucker: aboriginal plant use in central Australia*. IAD Press: Alice Springs.
- McKeown, K.C., 1944. *Insect wonders of Australia*. Angus and Robertson: Sydney.
- Meyer-Rochow, V.B., 1975. Local taxonomy and terminology for some terrestrial arthropods in five different ethnic groups of Papua New Guinea and Central Australia. *Journal of the Royal Society of Western Australia* 58: 15-30.
- New, T.R., 1995. *Introduction to invertebrate conservation biology*. Oxford University Press: Oxford.
- Reid, J., Baker, L., Morton, S.R. and Mutitjulu Community, 1992. Traditional knowledge and ecological survey equals better land management. *Search* 23: 249-251.
- Sillitoe, P., 1995. Ethnoscience observations on entomology and mycology in the Southern Highlands of Papua New Guinea. *Science in New Guinea* 21: 3-26.
- Tindale, N.B., 1966. Insects as food for the Australian aborigines. *Australian Natural History* 15: 179-183.
- Tindale, N.B. 1981. Desert aborigines and the southern coastal peoples: Some comparisons. Pp. 1853-1884 in: Keast, A. (ed), *Ecological biogeography of Australia*. Dr. W. Junk: The Hague.

BIODIVERSITY INDICATORS IN CONTRASTING VEGETATION TYPES: A CASE STUDY FROM WESTERN AUSTRALIA

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Abstract

Abensperg-Traun, M., Arnold, G., Steven, D., Smith, G., Atkins, L., Viveen, J. and Gutter, M., 1997. Biodiversity indicators in contrasting vegetation types: a case study from Western Australia. *Memoirs of the Museum of Victoria* 56(2): 637–641.

Vegetation structural diversity, species richness of plants, terrestrial arthropods and lizards, and the relative abundance of species within ant functional groups, were examined as indicators of faunal richness in gimlet (*Eucalyptus salubris*) woodlands (29 sites) and shrublands (27 sites) in semi-arid, agricultural Western Australia. Sites varied in grazing history (woodland) and in farming history (shrubland).

Total faunal richness was not effectively predicted by any indicator variable for either vegetation type. Vegetation structural diversity and richness of plants were effective indicators of the richness of some faunal groups in woodland but not in shrubland. Structural diversity explained 73% (+ve) of the pooled richness of scorpions + termites + lizards in woodland. In shrubland, no variable explained > 25% of the richness of any faunal group. Reasons for the differences in the predictive qualities of structural diversity and plant richness between the vegetation types are discussed.

Introduction

The loss of biodiversity (e.g., species richness) at all spatial scales must be of concern to all Australians. One of the issues that needs to be addressed by biologists is the identification of efficient indicators of biodiversity (Oliver and Beattie, 1993; Andersen, 1995; Majer and Beeston, 1996), such as vegetation structure or plant richness, because these are easy and hence cost-efficient to measure. With the exception of simple ecosystems, such as rehabilitated mine-sites (Majer, 1983), Australian studies give little hope for a quick solution to the search for effective biodiversity indicators (e.g., Yen, 1987; Oliver, 1993). The present study is a condensed version of a wider investigation into biodiversity indicators in native vegetation remnants in the Western Australian wheatbelt (Abensperg-Traun et al., 1996). It tests the qualities of four indicators of the species richness of terrestrial arthropods and lizards in two contrasting native vegetation types: 1, vegetation structural diversity; 2, species richness of native plants; 3, the richness of other faunal groups; and 4, the abundance of individual species within ant functional groups.

Methods

Study area and study sites

The study was carried out between 1991 and 1994, in a 1680 km area of the central wheatbelt of southwestern Western Australia (near 31°25'S, 117°26'E). Descriptions of the study area were given by Beard (1980), McArthur (1993) and Saunders et al. (1993). We selected eucalypt woodland (gimlet *Eucalyptus salubris*, 29 sites) and shrubland vegetation (27 sites) because these are major vegetation types in the study area and because they represent a range of disturbance histories. Most woodland sites have been grazed, and most shrubland sites have been farmed for varying periods and abandoned at least 20 years ago, and have regrown to varying degrees (Arnold and Weeldenburg, 1991). Sample areas were 0.25 ha for arthropods, 1 ha for lizards, and 400 m² for plants.

Data collection

Vegetation structural diversity was measured once (mid-winter) using subjective scores from 1 = low abundance of a structural component (< 10% cover), 2 = moderate abundance of a structural component (10–30% cover), 3 = high

abundance of a structural component (30-70% cover), 4 = very high abundance of a structural component (> 70% cover) for three components: living vegetation (native trees, shrubs, grasses); litter; standing and fallen dead wood. All scores were then summed to give an overall score of structural diversity for each site.

Plant species richness, measured once (spring), is the total number of native vascular plant species recorded within a 20 x 20 m site, located centrally within the fauna sampling area.

Differences between woodland and shrubland study sites in arthropod taxa selected for study are due to logistics, particularly the lizards, and to differences in the richness and abundance of the taxonomic groups. For woodlands, we studied scorpions, termites, beetles, ants and lizards; for shrublands, we studied termites, beetles, hemipterans (bugs, leafhoppers, cicadas), ants and butterflies. Sampling procedures followed standard techniques using pitfall traps (16 plastic cups per site, each 90 mm wide and 110 mm deep, opened for seven consecutive days) and hand collections (termites, butterflies, lizards). With the exception of woodland beetles which were sampled across four seasons, all other samples are from summer collections. For identification to species/morphotype level, specimens were matched with reference collections for the study area (scorpions, termites, ants), or using published keys (beetles, hemipterans, butterflies, lizards). Ant species were also placed into functional groups (Andersen 1990).

Data analysis

Correlation analysis was used to examine the relationships between faunal richness variables,

and between faunal richness and vegetation structural diversity and plant richness. Relationships between the abundance of ant species within functional groups and the richness of other faunal groups were analysed in a principal components regression. Principal component scores of ant functional groups were used as new independent variables in the regression. A forward step-wise (linear) procedure was used where the model fits the constant and then adds the most significant indicator variables in a step-wise fashion. A backward procedure produced similar results.

Results

Vegetation structural diversity and plant species richness

Total faunal richness was poorly predicted by structure or plant richness in either vegetation type (Table 1). Structural diversity and species richness of plants were effective indicators of a subset of the fauna in gimlet woodlands, but explained low percentages of the variation in richness of shrubland faunal groups (Table 1). In woodland, the highest percentages explained were 55% for termites (structure, +ve), 52% for beetles (structure, -ve), 40% for scorpions (structure, +ve) and 56% for lizards (plant richness, +ve) (Table 1). Structural diversity explained 73% of the pooled richness of scorpions + termites + lizards (Figure 1).

Structural diversity was not significantly correlated with any shrubland arthropod richness variable. Plant richness was significantly correlated with beetle and butterfly richness but explained low percentages of the variation in richness (14% and 20%, respectively) (Table 1).

Table 1. Correlation coefficients (r) between the richness of faunal groups and vegetation structural diversity and native plant richness. * $P < 0.05$, *** $P < 0.001$; ns not statistically significant; — not sampled.

Taxa	Structural diversity		No. native plant species	
	Woodland	Shrubland	Woodland	Shrubland
Scorpions	+0.63***	—	+0.69***	—
Termites	+0.74***	ns	+0.59***	ns
Hemipterans	—	ns	—	ns
Beetles	-0.72***	ns	-0.45*	-0.37*
Butterflies	—	ns	—	+0.45*
Ants	ns	ns	+0.46*	ns
Lizards	+0.42*	—	+0.75***	—
All taxa	+0.38*	ns	+0.57***	ns

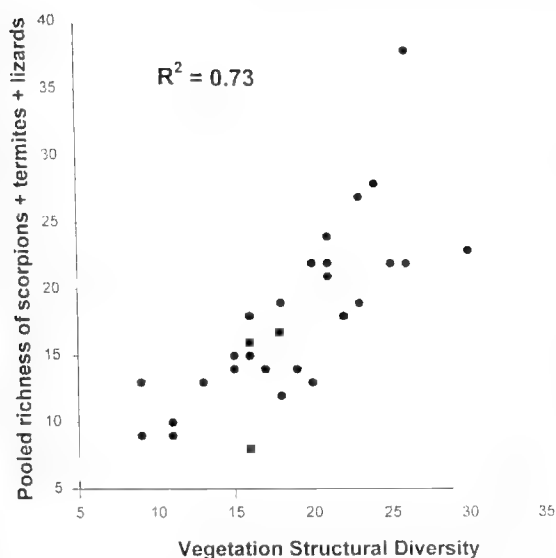


Figure 1. Relationship between the pooled richness of scorpions + termites + lizards and the structural diversity of the vegetation.

Species richness of other fauna

Total faunal richness was poorly predicted by any faunal richness variable in either vegetation type (Table 2). More woodland faunal richness variables were significantly intercorrelated than in the shrubland fauna (Table 2). Highest correlations in woodlands were between termites and beetles (40% of variation explained), lizards and scorpions (31% explained) and scorpions and total species richness (30% explained) (Table 2). Scorpions were thus the best predictors of the richness of other fauna.

In shrubland, only richness of termites and hemipterans were significantly correlated with ants and total arthropod richness but explained low percentages of the variation (18% and 21%, respectively) (Table 2).

Abundance of ant functional groups

Total faunal richness, or the richness of any faunal group, was poorly predicted by the abundance of ant functional groups in either vegetation type. Highest percentages of total faunal richness explained by ants were 36% for woodlands (dominant dolichoderine ant spp.) and 27% for shrublands (opportunistic ant spp.) (Table 3). Numbers of significant correlations, and percentages of the variation explained, were greater for woodland than for shrubland faunal groups (Table 3).

Discussion

Poor prediction of total faunal richness by any indicator variable follows a pattern found for studies in other Australian ecosystems (e.g., Yen, 1987; Oliver and Beattie, 1993). Observed differences between the vegetation types in the predictive qualities of vegetation structural diversity and plant richness may be due to differences in sampling regime, disturbance history, species composition of the fauna, biogeographic characteristics of study remnants, the way structure was measured, or simply because these are two very different systems and thus behave differently.

The woodland and shrubland data sets are comparable in numbers of study sites (29 sites as against 27 sites), trap size and density/m (identical), assessment of vegetation structural diversity (identical), and assessment of the richness of plants, termites and ants (identical). Beetles were sampled more intensively in woodland (4 seasons as against 1 season) and therefore provide no valid comparison across the two vegetation types.

Woodland remnants have a simple structure of the vegetation (and species-poor floristics), the major disturbance is livestock-grazing, and the remnants are small in area (mostly < 5 ha) and high in spatial isolation (Arnold and Weeldenburg, 1991). Shrublands, in contrast, are highly complex in structure (and floristics), they are largely ungrazed but some have been farmed for varying periods before abandonment (> 20 years ago), and they are larger in area (mostly > 20 ha) and lower in spatial isolation (Arnold and Weeldenburg, 1991). In addition to these different physical and biological characteristics of the vegetation types, the faunal groups differ in species composition and in their responses to disturbance (Lobry de Bruyn, 1993; Abensperg-Traun et al., 1996). Taken together, these differences may account for the discrepancy in the efficiency with which faunal richness was predicted in the two vegetation types.

Also, using the same scale of measurement of structure for two structurally very different vegetation types may not have been appropriate. In contrast to the woodlands, the shrublands of south-west Western Australia are renowned for their high alpha- and beta-diversity of plants (Lamont et al., 1984). Reasons given for this high spatial diversity are a complex underlying geology, small-scale changes in soil characteristics, and disturbance histories such as fire (Bell et al., 1984; Lamont et al., 1984). The qualities

Table 2. Correlation coefficients (r) between the richness of individual faunal groups. *P < 0.05, **P < 0.01, ***P < 0.001; ns not statistically significant.

	Scorpions	Eucalypt woodland		Ants	Lizards
		Termites	Beetles		
Scorpions	—				
Termites	+0.53**	—			
Beetles	-0.37*	-0.63***	—		
Ants	+0.50**	+0.41*	ns	—	
Lizards	+0.56**	+0.38*	ns	ns	—
All other taxa	+0.54**	ns	ns	ns	ns

	Termites	Shrubland		Butterflies	Ants
		Hemipterans	Beetles		
Termites	—				
Hemipterans	ns	—			
Beetles	ns	ns	—		
Butterflies	ns	ns	ns	—	
Ants	-0.42*	ns	ns	ns	—
All other taxa	ns	+0.44*	ns	ns	ns

Table 3. Summary of step-wise regression (on principal component scores) using the abundance of individual ant species within functional groups as indicators of faunal richness. Values are percentage variation accounted for.

Ant functional groups	Eucalypt woodland		Beetles	Lizards	Total species excl. ants
	Scorpions	Termites			
Dominant Dolichoderinae	18	ns	27	42	36
Sub-ordinate Camponotini	42	26	ns	ns	31
Hot-climate specialists	28	22	ns	ns	ns
Cryptic spp.	23	23	19	18	16
Opportunist spp.	25	ns	ns	ns	ns
Generalized myrmicine spp.	42	37	25	21	24

	Shrubland		Beetles	Butterflies	Total species excl. ants
	Termites	Hemiptera			
Dominant Dolichoderinae	ns	22	ns	ns	26
Sub-ordinate Camponotini	ns	ns	ns	ns	ns
Hot-climate specialists	ns	27	ns	ns	25
Cryptic spp.	ns	ns	ns	ns	ns
Opportunist spp.	ns	ns	30	ns	27
Generalized myrminine spp.	16	ns	ns	ns	ns

Footnote. Dominant Dolichoderinae = *Iridomyrmex* spp.; Subordinate Camponotini = *Camponotus* spp., *Polyrhachis* spp.; Hot-climate specialists = *Melophorus* spp., *Meranoplus* spp.; Cryptic spp. = *Tapinoma* sp., *Stigmacros* spp.; Opportunists = *Rhytidoponera* spp., *Tetramorium* spp.; Generalized myrmicine spp. = *Pheidole* spp., *Monomorium* spp., *Crematogaster* spp.

of any one habitat component as a predictor of faunal richness is likely to decline with an increase in structural/floristic diversity of the vegetation (MacArthur, 1964).

Using vegetation structural diversity and plant richness as predictors of the richness of scorpions, termites and lizards in gimlet woodlands for comparable vegetation types elsewhere in Australia is limited, first, by geographic variations in their abundance and richness. Second, associated with such spatial variations are changes in the interactions between biotic groups, particularly the ants which are known to influence the abundance and richness of other arthropods. Third, disturbance type or intensity may influence the bioindicator quality of any one variable, yet disturbance effects on flora and fauna may vary with vegetation type, soil type, climate or life-history strategies of target biota (e.g., Grubb, 1977; Hobbs and Huenneke, 1992). The use of structural diversity or plant richness as faunal indicators for different vegetation types, or for vegetation types with different disturbance histories, or for different geographic or climatic regions, should not be adopted without verification of their validity.

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References

- Abensperg-Traun, M., Arnold, G.W., Steven, D.E., Smith, G.T., Atkins, L., Viveen, J.J. and Gutter, M., 1996. Biodiversity indicators in semi-arid, agricultural Western Australia. *Pacific Conservation Biology* 2: 375–389.
- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–357.
- Andersen, A. N., 1995. Measuring more of biodiversity: genus richness as a surrogate of species richness in Australian ant faunas. *Biological Conservation* 73: 39–43.
- Arnold, G. W. and Wceldenburg, J. R., 1991. *The distribution of remnant native vegetation in parts of the Kellerberrin, Tammin, Trayning and Wyalkatchem shires of Western Australia*. Technical Memorandum No. 33, CSIRO, Division of Wildlife and Ecology, Perth.
- Beard, J.S., 1980. *The vegetation of the Kellerberrin area, Western Australia*. Vegmap Publications: Perth.
- Bell, D.T., Hopkins, A.J.M. and Pate, J.S., 1984. Fire in Kwongan. Pp. 178–204 in: Pate, J.S. and Beard, J.S. (eds), *Kwongan. Plant life of the sandplain*. University of Western Australia Press: Nedlands.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107–145.
- Hobbs, R.J. and Huenneke, L.F., 1992. Disturbance, diversity and invasion: implications for conservation. *Conservation Biology* 6: 324–337.
- Lamont, B.B., Hopkins, A.J.M. and Hnatiuk, R.J., 1984. The flora. Composition, diversity and origins. Pp. 27–50 in: Pate, J.S. and Beard, J.S. (eds.), *Kwongan. Plant life of the sandplain*. University of Western Australia Press: Nedlands.
- Lobry de Bruyn, L.A., 1993. Ant composition and activity in naturally-vegetated and farmland environments on contrasting soils at Kellerberrin, Western Australia. *Soil Biology and Biochemistry* 25: 1043–1056.
- MacArthur, R.H., 1964. Environmental factors affecting bird species diversity. *American Naturalist* 98: 387–397.
- Majer, J.D., 1983. Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. *Environmental Management* 7: 375–383.
- Majer, J.D. and Beeston, G., 1996. The biodiversity integrity index: an illustration using ants. *Conservation Biology* 10: 65–73.
- McArthur, W.M., 1993. History of landscape development. Pp. 10–22 in: Hobbs, R.J. and Saunders, D.A. (eds.), *Reintegrating fragmented landscapes: towards sustainable production and nature conservation*. Springer-Verlag: New York.
- Oliver, I., 1993. Rapid biodiversity assessment and its application to fauna conservation in production forests. Pp. 31–34 in: *Rapid Biodiversity Assessment. Proceedings of the Biodiversity Assessment Workshop, 1993*. Macquarie University: Sydney.
- Oliver, I. and Beattie, A.J., 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* 7: 562–568.
- Saunders, D.A., Hobbs, R.J. and Arnold, G.W., 1993. The Kellerberrin project on fragmented landscapes: a review of current information. *Biological Conservation* 64: 185–192.
- Yen, A.L., 1987. A preliminary assessment of the correlation between plant, vertebrate and Coleoptera communities in the Victorian mallee. Pp. 73–88 in: Majer, J.D. (ed.), *The role of invertebrates in conservation and biological survey*. Department of Conservation and Land Management, Western Australia.

PANZER MITES ON THE FOREST PHYLLOPLANE

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Abstract

Barnes, V.M., 1997. Panzer mites on the forest phylloplane. *Memoirs of the Museum of Victoria* 56(2): 643–646.

The distribution and abundance of the phylloplane specialist, *A. polyphyllus*, appears to be influenced by architectural complexities of the leaf.

Introduction

Over the last decade, canopy fogging in a variety of tropical forests has changed our perception of the biodiversity of insects. However, most of these studies have probably underestimated both the abundance and species richness of a more obscure group of arthropods, the mites (Acari) (Walter and O'Dowd, 1995a). Usually considered denizens of the soil and litter, these tiny mites may exploit the wide variety of food resources and microhabitats (ranging from the leaf surface, or phylloplane, to bark crevices) available in the forest canopy (Walter et al., 1994; Walter and O'Dowd, 1995b). For example, the diverse Oribatida or 'Panzer mites' (a German term referring to their 'tank-like' exoskeleton) are typically stereotyped as a soil-dwelling group. Yet, some Panzer mites may lead arboreal lifestyles or even be microhabitat specialists within the forest canopy (Walter and Behan-Pelletier, 1993).

In forests in southeastern Australia, I studied the distributional ecology of one such oribatid mite, *Adhaesozetes polyphyllus* (Acari: Oribatida: Licneremaeoidea) asking three questions:

1. Is *A. polyphyllus* a phylloplane specialist?
2. Does the morphology of *A. polyphyllus* correlate with its arboreal lifestyle?
3. Is *A. polyphyllus* a habitat specialist at a larger scale, e.g., forest type?

Is *Adhaesozetes* a phylloplane specialist?

To determine whether *A. polyphyllus* specialised on any particular microhabitat in the forest canopy, I compared its distribution with that of other oribatid species across microhabitats (bark, stem & leaves) on four plant species and in the soil (Fig. 1). From one plant, four soil and leaf litter cores (7 cm by 4 cm), four bark and moss strips (8 cm by 2 cm), four stem sections (12–15 cm in length) and eight leaves were collected. The sampling numbers remained con-

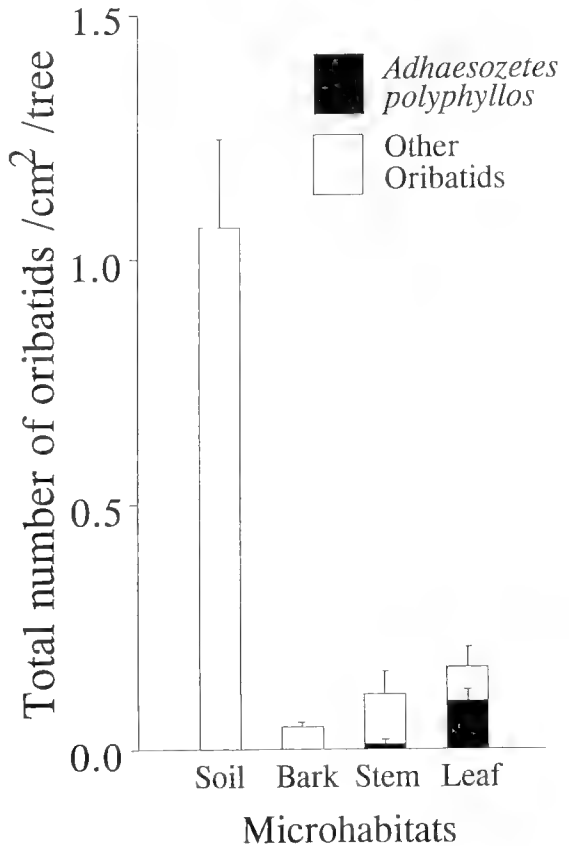


Figure 1. The mean number (\pm standard error) of *A. polyphyllus* (nymphs and adults combined) and other oribatid mite species per cm of microhabitat sample per tree. The tree species (Musk Daisy-bush, Silver Banksia, Snowy Daisy-bush, and Lilly-pilly) are pooled.

stant for the Musk Daisy-bush and the Snowy Daisy-bush. However, the number of leaf samples was increased to 20 for each of the Lilly-pilly plants and the Silver Banksia plants, as the population densities were unknown. Shoots,

approximately 7 cm in length, were collected from the Silver Banksia to represent leaves as this plant species had considerably smaller leaves than the other three species.

The four microhabitats within the tree were not directly comparable. One way to equalise the comparison was to transform the numbers of mites per cm. As expected, the abundance and species richness of oribatid species was greatest in the soil. On a per cm basis, the mean number was almost ten times greater in the soil than any of the plant microhabitats (bark, stem, and leaf) sampled. Of the oribatid species on the phylloplane, *A. polyphyllos* (mean total length: male c. 400 µm, female c. 430 µm) was the most abundant on all plant species sampled. Furthermore, all life stages of *A. polyphyllos* were abundant on the leaf surface and rare or absent in the other microhabitats (Fig. 2). With the exception of the Lilly-pilly (*Acmena smithii*), which has smooth leaves, *A. polyphyllos* and its remains (exuviae) were almost entirely restricted to the phylloplane. My results and observations show that *A. polyphyllos* lives, eats, reproduces, and dies on the forest phylloplane.

Although *A. polyphyllos* occurred on the leaves of all plant species examined, its abundance varied between plant species. Some of this variation could be explained by the differences in the leaf surface features. For example, the 'forest' of trichomes (leaf hairs) found on the Musk Daisy-bush (*Olearia argophylla*), Silver Banksia (*Banksia marginata*) and Snowy Daisy-bush (*Olearia lirata*) may provide footholds for attachment, and protection from the elements and predators. Additionally, trichomes may trap fungal spores and pollen, which are important foods for many oribatid species. In contrast, the smooth, 'desert-like' surface of the Lilly-pilly may not provide the architectural complexity that may be necessary for an arboreal lifestyle.

Does the morphology of *Adhaesozetes* correlate with its arboreal lifestyle?

Life on the phylloplane presents several hurdles. The morphological characteristics of *A. polyphyllos* may aid in its arboreal lifestyle. Firstly, its tarsal claws, and adhesive pulvilli may anchor the mite to the phylloplane by attaching to surface irregularities. Secondly, its dorsoventrally flattened body may help it to remain within a narrow boundary layer, aiding with water balance. A flattened body shape would also reduce the chances of dislodgment by wind or by leaves rubbing together.

Life on the phylloplane may also present difficulties in obtaining adequate food, and in avoiding competition and predation. Trichomes may aid in trapping fungal spores, and competition and predation may be reduced as there are fewer mites on the phylloplane compared with the soil. The thick, hard exoskeleton of *A. polyphyllos* may protect adults from predators, and the bothridial sensillum (thought to be an 'anemoreceptor' sensing movement of air currents) may enable these blind mites to sense movements of nearby predators.

The morphological characteristics of *A. polyphyllos* are consistent with other arboreal oribatid species and distinct from soil-dwelling ones, suggesting morphological correlates with an arboreal habit. Furthermore, these arboreal oribatid species are taxonomically distinct from their relatives in the soil.

Is *Adhaesozetes* a habitat specialist at a larger scale?

The architectural complexity of the phylloplane appears to influence the distribution and abundance of *A. polyphyllos*, but do habitat differences at a larger scale, that is, forest type, also play an important role? To answer this question, I sampled 20 leaves from eight Musk Daisy-bushes in wet sclerophyll forest and rainforest at three different sites. The distribution and abundance of *A. polyphyllos* did not differ significantly between forest habitats. The apparent preference of *A. polyphyllos* for the wet sclerophyll forest (Fig. 3A) may be explained by the distribution and abundance of the Musk Daisy-bush, a preferred plant species. It is a wet sclerophyll forest specialist and a coloniser of disturbed areas, which are more common in wet sclerophyll forest than rainforest.

In addition, I sampled a variety of plant species in three forest types, dry sclerophyll forest, wet sclerophyll forest, and warm temperate rainforest. These results (Fig. 3B) differed only slightly from the above survey. All life stages of *A. polyphyllos* were distributed across all three forest types and its abundance did not differ significantly between forest habitats. Independent of forest type, mites and their exuviae were more common on plant species with leaf trichomes, such as the Musk Daisy-bush and ferns. Thus, the distribution and abundance of *A. polyphyllos* appears more strongly related to the fine-scale differences in leaf surface structure within forest types than coarse-scale differences in forest type itself.

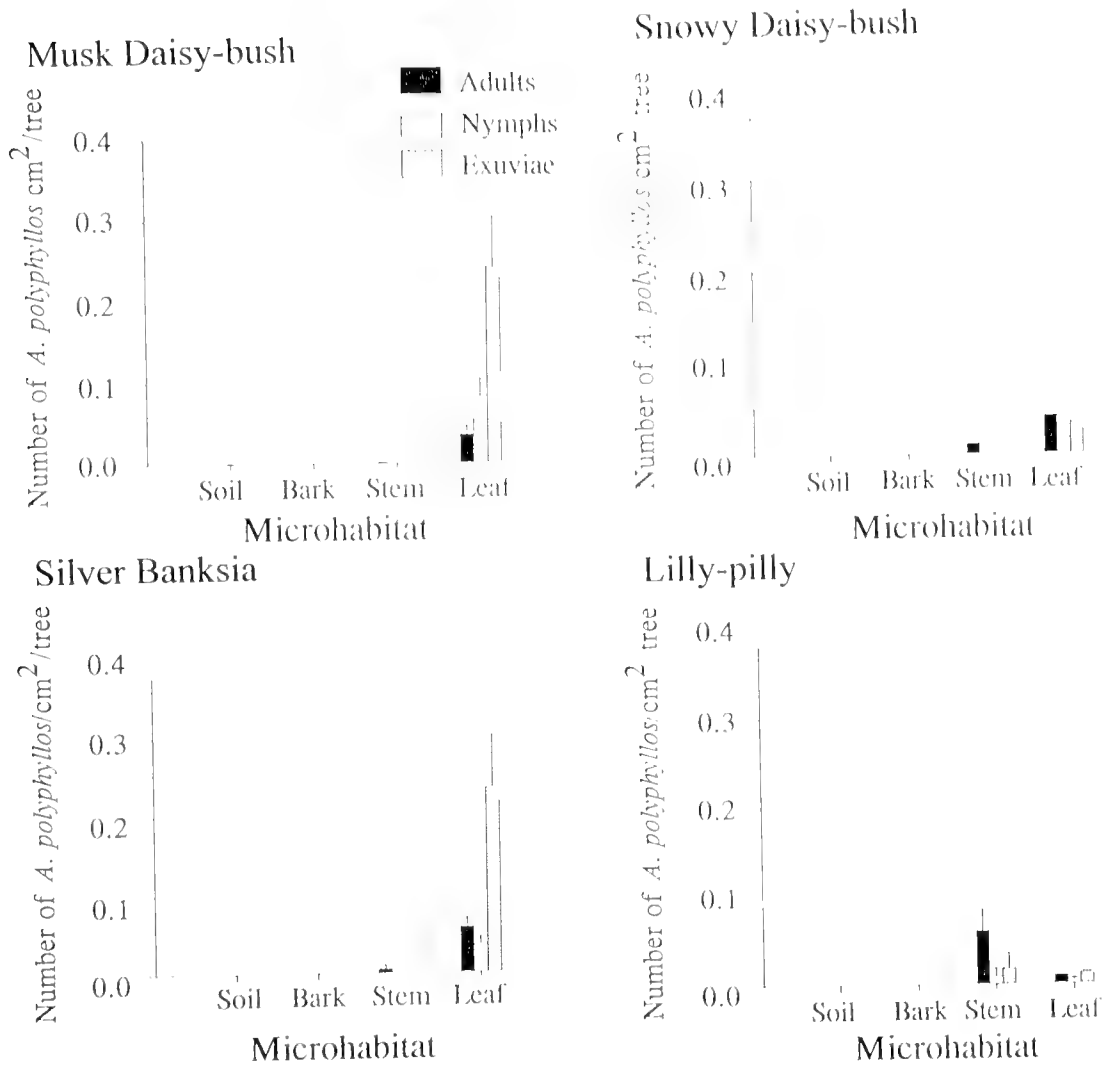


Figure 2. The abundance of *A. polyphyllus* (mean no. $\text{cm}^{-2} \text{ tree}^{-1} \pm \text{SE}$) on the Musk Daisy-bush ($N = 15$ trees), Silver Banksia ($N = 3$), Snowy Daisy-bush ($N = 1$) and Lilly-pilly ($N = 3$).

Conclusions

Adhaesozetes polyphyllus is an arboreal mite and a specialist on the leaf surface. All life stages (eggs, nymphs, and adults) were abundant on the phylloplane, while few if any individuals were found in the three other microhabitats. The abundance of exuviae on the phylloplane suggests that the development of the life stages occur there. Furthermore, *A. polyphyllus* has morphological characteristics (well-developed

tarsal claws, adhesive pulvilli, club-shaped bothridial sensillum, and a dorsoventrally flattened body) consistent with an arboreal habit. These appear to be consistent with other arboreal oribatid species and distinct from soil-dwelling ones.

Within the forest types examined, fine-scale differences in leaf structural complexity (including trichomes, raised midrib and veins) appear to have a larger effect on the distribution and abundance of *A. polyphyllus* and other oribatid

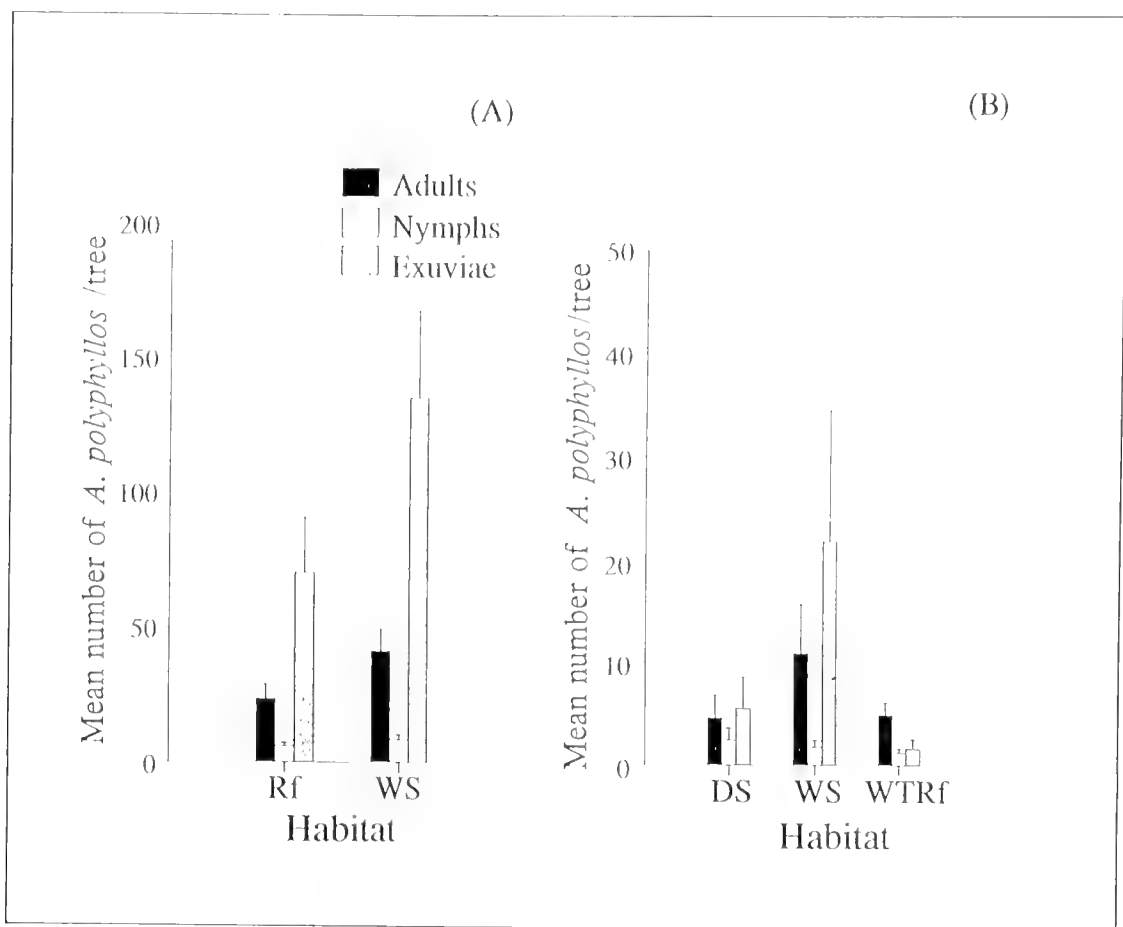


Figure 3. The mean number of *A. polyphyllus* per tree (\pm SE) on (A) the Musk Daisy-bush in rainforest (Rf) and wet sclerophyll forest (WS) (N = 24 trees in each forest type pooled across three sites). (B) The abundance of *A. polyphyllus* (mean number per tree \pm SE) pooled across a variety of plant species sampled in dry sclerophyll forest (DS), wet sclerophyll forest (WS) and warm temperate rainforest (WTRf) (N = 30 trees in each forest type pooled across two sites).

species than coarser scale differences in forest type. Phylloplane specialists, like *A. polyphyllus* appear to select those plant species that offer them 'mite-sized' architectural complexity which may help them to overcome the substantial hurdle of a phylloplane existence.

References

- Walter, D.E. and Behan-Pelletier, V., 1993. Systematics and ecology of *Adhaesozetes polyphyllus*, sp. nov. (Acari: Oribatida: Licneremacoidea) leaf-inhabiting mites from Australian rainforests. *Canadian Journal of Zoology* 71: 1024–1040.
- Walter, D.E. and O'Dowd, D.J., 1995a. Life on the forest phylloplane: hairs, little houses, and myriad mites. Pp. 325–351 in Lowman, M. D. and N. M. Nadkarni (eds.), *Forest canopies*. Academic Press: San Diego.
- Walter, D.E. and O'Dowd, D.J., 1995b. Beneath biodiversity: factors influencing the diversity and abundance of canopy mites. *Selbyana* 16: 12–20.
- Walter, D.E., O'Dowd, D.J. and Barnes, V., 1994. The forgotten arthropods: foliar mites in the forest canopy. *Memoirs of the Queensland Museum* 36: 221–226.

INVERTEBRATE PATHOLOGY: A DEVELOPING AND ESSENTIAL SCIENCE FOR INVERTEBRATE CONSERVATION

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Abstract

Cunningham, A.A., 1997. Invertebrate pathology: a developing and essential science for invertebrate conservation. *Memoirs of the Museum of Victoria* 56(2): 647-648.

The captive breeding and reintroduction of endangered invertebrate species is increasingly being carried out by zoos and other conservation organisations. Veterinary involvement in the captive care of invertebrates, including disease investigation and screening for normal and abnormal micro-organisms, can result in improving not only the welfare of the animals but also the conservation value of the breeding programmes concerned.

Invertebrates comprise over 90% of the described animal kingdom and possibly greater than 99% of all animals on earth. For a variety of reasons, including a growing awareness of their ecological importance and vulnerability, endangered species of invertebrate are being increasingly kept in zoological collections. Concurrent with this is a growing requirement to improve the husbandry, including medicine, of these animals. Research into invertebrate diseases is not new, but such work has largely been in the field of pest control or of studies on basic physiology. Little attention has been paid to diagnostic pathology other than work on certain groups which are of obvious economic importance, such as certain molluscs. In these cases the approach has been to investigate disease at the level of the population rather than the individual animal. However, with the captive breeding of endangered species, the individual invertebrate may be as important as any other (vertebrate) animal in a similar situation.

The diagnosis of infectious disease is particularly difficult when working with invertebrates due to the lack of information on the normal micro-flora and -fauna of the animals. One way to help investigate this is to examine healthy free-living animals of the same species (and from the same geographical area) as those in captivity, but usually this is not possible. At the Zoological Society of London (ZSL) often we try to screen freshly wild-caught invertebrates in order to learn something of their normal commensal micro-organisms, but this also may be impractical for a variety of reasons, not least because of the costs involved, both in time and money. However, such information is very important, particularly if the animals, or their offspring, are

destined for eventual release (see below). Future trends are likely to be to carry out much more of this type of fundamental work, both at ZSL and other collections.

In recent years, the Zoological Society of London has been increasingly involved in captive breeding and release programmes for endangered species of invertebrate and, at the same time, we have been developing approaches to investigating disease in our captive populations. This has involved both the development of diagnostic and therapeutic techniques and the creation of computerised record systems that enable trends in fecundity, growth rates and mortality to be analysed (Burlingham-Johnson, 1994). Such data are essential if optimum husbandry techniques are to be employed and signs of early or subclinical disease are to be detected. Although the individual treatment of animals is considered to be conventional for vertebrates, it still is regarded as unusual for invertebrates. However, at ZSL we have had some successes in the individual treatments of insects in the face of disease epidemics, such as the treatment of Olympia's ground beetles (*Chrysocarabus olympiae*) with antifungal drugs (Cunningham and Frank, 1993).

There is a growing awareness of the dangers of the accidental introduction of alien parasites when translocating animals (Cunningham, 1996), and this applies equally whether the target species has an internal or an external skeleton. The science of pathology has a major role to play in this area of wildlife conservation. For example, at ZSL we postponed a release programme for the wart-biter cricket (*Decticus verrucivorus*) when the colony destined for release was found to be infected with a fungus. Simi-

larly, the reintroduction of captive-bred English field crickets (*Gryllus campestris*) was stopped when, on routine pre-release screening of sacrificed nymphs, the animals were found to be infected with a protozoan parasite of unknown origin. Of course, should this parasite turn out to be natural to the wild population, then the release programme can be recommenced.

In conclusion, it is important that zoological collection managers and others are aware that veterinary involvement in the captive care of invertebrates can result in improving not only the welfare of the animals but also the conservation value of the breeding programmes concerned. If the commitment to wildlife conservation by such institutions is to be taken seriously then resources must be allocated accordingly. This is an exciting area for zoos and zoo vets and there is much work to be done.

References

- Burlingham-Johnson, A., Clarke, D. and Pearce-Kelly, P., 1994. CERCIC(c): a computer system for the demographic and genetic analysis of captive invertebrates, fish and other populations of colony animals. *International Zoo Yearbook* 33: 278–283.
- Cunningham, A.A., 1996. Disease risks of wildlife translocations. *Conservation Biology* 10(2): 349–353.
- Cunningham, A.A. and Frank, J.M., 1993. Veterinary observations on an arthropod mycosis with comparison of the efficacy of topical povidone-iodine, nystatin and clotrimazole treatments. *Journal of Zoo and Wildlife Medicine* 24(4): 508–514.

INVERTEBRATE BIODIVERSITY AND CONSERVATION IN TASMANIAN CAVES

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Abstract

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Tasmanian caves support a diverse invertebrate fauna, representing the richest known assemblages of cave obligate species in temperate Australia. Current studies have yielded much valuable and unusual information regarding spider, amphipod and cricket species in particular, while highlighting their sensitivity to environmental disturbance.

Introduction

Cave ecosystems offer unique opportunities to evolutionary biologists because of their often highly adapted fauna combined with their well-defined abiotic environmental parameters. Despite its barren appearance and slow rate of change, the cave environment can be remarkably speciose, and Tasmanian caves have recently been identified as hosting the richest assemblages of cave obligate invertebrates in temperate Australia (Eberhard et al., 1991). This high biodiversity combined with Tasmania's location at a climatic and geographic extreme, and its relative abundance of undisturbed sites, makes the region extremely valuable for the study of the evolutionary history of Australian cave biota.

In Tasmania as elsewhere, however, land management and land degradation problems pose a significant danger to caves and their fauna. Current studies of the life cycles of certain cave animals have highlighted their susceptibility to environmental disturbance (Richardson et al., in press, and our unpublished data), while at the same time indicating both the practical benefits that further study may provide, and the high scientific and conservation values of these delicate ecosystems.

General background

The deceptive first impression that caves are depauperate is based on a combination of the small size of many cave organisms, their frequently sparse distributions, and their cryptic nature, since animals more frequently occur in the smaller cracks, crevices, and folds of cave formations to which human access is severely

limited. In Tasmania, the barren appearance of caves is increased by the absence of any major vertebrate usage; roosting bats and birds are not present (most probably due to the low temperature of Tasmanian caves), nor are any cave fish known. The only visiting vertebrates are humans and the occasional rodent, macropod, or snake seeking shelter. In spite of this, Tasmanian invertebrate cave assemblages are amongst the richest known in temperate zone Australia.

Cave animals, or **cavernicoles**, are essentially a heterogeneous assemblage occupying different regions of caves, and their classification is based around their relationship to particular cave zones. While there are many systems for such classification, the simplest (Vandel, 1965; with expansion by Howarth, 1983) divides animals into four groups as follows.

Troglobites are obligate cave species, strictly adapted to subterranean habitats and unable to survive outside them. These animals often display a large suite of distinctive morphological, physiological, and behavioural adaptations, many quite bizarre, and their domain is that of the deep cave.

Troglophiles are facultative cavernicoles that commonly live and reproduce in caves, but are not totally confined to them; they may be found in similar sheltered, cool, dark and humid epigeal microhabitats.

Trogloxenes are occasional cavernicoles that regularly inhabit caves, usually near the entrance, for refuge and a favourable microclimate, but must periodically return to the surface to feed, usually at night. Such animals often require direct access to both the epigeal and hypogeal environments in order to survive.

Accidentals are surface animals which wander, fall, or are washed into caves, but cannot survive there.

Examples of the first three of these groups are presented in the following section.

Components of the Tasmanian cave fauna

The cavernicolous fauna of Tasmania consists of five major phyla, Platyhelminthes, Nemertini, Aschelminthes, Annelida, and Arthropoda, with the arachnids, crustaceans, and insects being particularly well represented (Eberhard et al., 1991). Ninety percent of the recorded Tasmanian cave genera are arthropods, and most of the cave obligate species belong to this phylum. In the course of numerous cave studies and surveys carried out by the authors, the following groups have received particular attention.

Spiders (Araneae)

Tasmanian caves support an interesting and diverse spider fauna, including *Hickmania troglodytes* (the Tasmanian Cave Spider) which is a troglophile, and an un-named amaurobiid spider, which is a troglobite.

Hickmania troglodytes (Family Austrochilidae) is the largest spider in Tasmania, with a leg-span of up to 18 cm when fully grown, and constructs a web of up to 120 by 60 cm. Endemic to Tasmania, and the only known species in the genus, *H. troglodytes* is of high systematic and zoogeographic interest. Its closest relatives live in Chile and Argentina, and it is of considerable evolutionary significance as it possesses major physical traits of both the primitive (liphistiomorph and mygalomorph) and advanced (araneomorph) spider groups. While the species is no longer considered a direct evolutionary link between these groups, it is considered one of the closest araneomorphs to the ancestral spider type from which they all diverged (Marples, 1968).

Hickmania troglodytes builds large pear shaped egg sacs which hang from the roof and sides of the cave. The young take approximately nine months to emerge from these sacs, a period significantly longer than the one to two months typical of epigean spiders, and their lifespan may cover decades (Doran, unpublished data). The egg sacs themselves are of intricate internal design and are highly resistant to fungal growth, which can over-run other organic materials in caves in a matter of days or even hours. A very ancient member of the Tasmanian fauna, *H. troglodytes*' stronghold is the twilight and transition (early) zones of caves, which may have

ensured the animal's survival during the rapidly fluctuating conditions of the Pleistocene (Goede, 1967).

In contrast, very little has yet been discovered about the troglobitic amaurobiids (Family Amaurobiidae), which inhabit deeper parts of the cave not prone to external seasonal influence. These spiders do not spin webs, but wander widely, although they may display some degree of territoriality (our unpublished data). The amaurobiids are often locally abundant, and the juveniles at least are depigmented and display some degree of eye reduction (M. Gray, pers comm.).

Amphipods (Malacostraca)

Several genera and species of troglobitic amphipods in the Superfamily Crangonyctoidea inhabit streams and pools in Tasmanian caves. The stream dwelling *Antipodeus* sp. (Family Paramelitidae), the generic placement of which is currently under review (W.D. Williams, pers comm.), is a **stygobiont**: an obligate groundwater dweller, or aquatic troglobite. It is found at several sites in northern Tasmania, including Little Trimmer Cave at Mole Creek (see following section). In contrast to terrestrial troglobites, this species displays distinct seasonal tendencies, and its lifecycle appears to be almost directly dependent upon the yearly changes in stream flow. Mating occurs from late-winter to spring, and over the summer months the amphipods may display protective burrowing behaviour prior to stream drying (our unpublished data). This burrowing allows the amphipods to survive seasonal dry spells, and appears to be triggered (perhaps by increasing calcium concentrations in the water) before the pools dry. These amphipods generally feed on detritus that is carried in by the stream, although different size classes appear to have their own preferences amongst the selection that this material offers.

Crickets (Orthoptera)

Cave crickets (Family Rhaphidophoridae) are easily the most common troglloxenes in Tasmania, the two main genera being *Micropathus* and *Parvotettix*. While species from both genera may inhabit the same cave, species from the same genus appear not to coexist (Eberhard et al., 1991). *Micropathus* species are most common in the moister western and southern parts of Tasmania, where they are established in large colonies, and the distribution and derivation of the species-complexes may have been influenced by Pleistocene glaciation (Richards, 1971a). Cave crickets are generally omnivorous,

and leave the cave at night to feed on forest floor invertebrates and materials (Barr, 1968), although they may also prey on juvenile spiders within the cave (our unpublished data). To adult spiders, beetles and other animals, the crickets provide a major source of food input to the cave, either directly as prey, or through their droppings and eggs. The latter are buried in silt banks of the deep cave, and possibly provide the sole food source for troglobitic beetles specially adapted to retrieve them.

Major sites and regions examined

In the Mole Creek region of northern Tasmania, 71 invertebrate taxa have been recorded from Kubla Khan and Genghis Khan caves (Eberhard, 1990b), including 3 species each of flatworms and springtails, 5 species each of annelids, myriapods and molluscs, 6 species of crustaceans, 21 arachnids and 23 insects. Although about 19 of these species were accidentals, at least 11, and possibly more, are troglobitic. The diversity of species recorded here is by far the highest for any single Tasmanian cave (Eberhard et al. 1991).

Precipitous Bluff, far southern Tasmania, supports the richest assemblage of cave obligate species presently known in temperate zone Australia, with at least 15 troglobitic or stygobiontic species recorded among a total cave fauna of some 32 (++) species (Eberhard et al., 1991). This area has the most highly cave adapted representatives in several animal groups, including amphipods, beetles, molluscs, and harvestmen, while the hydrobiid mollusc and opiloid (harvestmen) faunas are particularly notable for the diversity of species represented.

Ida Bay, far southern Tasmania, has 31 recorded cavernicolous species including 5 troglobites (21% of the fauna) from one survey (Richards and Ollier, 1976), and 30 species including 11 troglobites (36%) in another (Eberhard, 1990a). These figures exclude accidental or surface fauna, and cover such groups as the opiloid, pseudoscorpions, araneids, crustaceans, collembolans, hemipterans, and coleopterans amongst others (Eberhard et al., 1991).

Mount Anne (southern Tasmania) and Mount Ronald Cross (central to western Tasmania) support at least 5 and 3 troglobitic species respectively (Eberhard, 1987, 1989), while at Bubs Hill (western Tasmania) at least 6 definite troglobites and 6 other taxa of uncertain status have been recorded (Clarke 1989). Including accidentals, one cave in the Bubs Hill karst has

yielded over 55 taxa (Houshold and Clarke 1988).

Comparisons with temperate mainland Australia

Few data have been published for caves in temperate mainland Australia, but the literature includes over 6 troglobites from the Nullabor Plain (e.g., Richards, 1971b; Knott, 1983), at least 6 more from five cave areas in Victoria (Davey and White, 1986), 2 troglobites and 5 troglaphiles from Wombeyan Caves (Smith, 1982) and 2 species of troglaphile from Bungonia Caves in New South Wales (Wellings, 1977), and 25 species of aquatic cavernicole from a cave at Yanchep in Western Australia (although the number of stygobiontic species is not given; Jasinska and Knott, 1991). Against these figures, it would appear that Tasmania is comparatively rich in troglobitic diversity.

Conclusions

While data currently show that Tasmanian caves support substantially higher biodiversity than caves in temperate mainland Australia, such comparisons will remain rather crude until sampling strategies and sampling intensities can be in some way standardised, and until all karst areas have been surveyed. However, Tasmania is likely to remain an extremely rich source of cave fauna, whose age and diversity is related to the geology and geomorphic history of the karst systems in which it is found.

As caves are entirely dependent on outside sources for their energy input, and as their environments are slow to change and/or predictable, these ecosystems are highly vulnerable to external events, which may even occur at some distance from the caves themselves. Two major sources of food input, cricket guano and water carriage, are at high risk from land use practices that affect surrounding forest and water quality. Even the disruption of flow levels into the cave, whether by an increase or decrease, can have devastating effects on the cave fauna. While water levels may fluctuate enormously during the normal yearly cycle, this is generally predictable, and exceptionally severe conditions during the normal season are not as potentially catastrophic as relatively minor floods occurring at unusual times, or even the absence of floods at the expected time (Howarth, 1983).

More direct effects are also important. Caves may be heavily affected by quarrying, rubbish dumping, the in-filling of entrances or clearance

of surrounding land. Visitors are also a significant potential source of disturbance, and some cave inhabitants and habitats are particularly vulnerable to them (Richardson et al., in press). Indirect disturbance alone, such as light or movement, can disturb cave spiders and disrupt courtship and mating. Spiders may desert their egg sacs if disturbed frequently, which probably accounts for the rarity of these animals in tourist caves. Seepage pools supporting rare syncarid shrimps (Family Psammaspididae) can be destroyed by a single careless footstep, as can silt banks which support many of the small terrestrial invertebrates deep in caves. The cave environment is a very special, fragile habitat, into which even scientific visits should be carefully regulated to reduce potential, and very real, impacts.

Future directions: the Little Trimmer Cave Biological Monitoring Program — a model study

A faunal study designed to be of low impact was specifically formulated for Little Trimmer Cave at Mole Creek, Tasmania, in 1990. This program was established at the cave at the beginning of 1991 and is still ongoing today.

Little Trimmer Cave is a well decorated, stream bearing cave of reasonable length (the major passage is approx. 200 m). Situated in State forest, it has been gated by the Tasmania Forestry for several years, so that access is limited to facilitate scientific studies in an undisturbed hypogean environment. Visits are regular and infrequent (ranging from monthly to bimonthly), visitor numbers are restricted, and studies are designed around conservation of the cave environment and its fauna. Movement through the cave is kept smooth and quiet to minimise disturbance due to noise and sudden vibration, and in all but the most carefully considered cases the introduction of any foreign matter, particularly organic, volatile, or odorous substances which may attract or repel cavernicoles, is avoided. Pathways are marked by string to reduce the area exposed to disruption by researchers traversing the cave, and the greatest care is taken to avoid even the smallest animals and cave formations on and above these paths. Substrate Protection Zones are established throughout the cave to preserve the more fragile habitats and subcommunity types, and study of the fauna is conducted by census, marking, and careful observation. With a strict regime of capture, measurement, description

and release, the impact on the fauna is minimal. Records are also kept of the date, duration, party number, and course taken through the cave for each visit, so that the impact on the cave environment of even these few visits can be assessed.

The benefits of this monitoring strategy have been many. Little Trimmer Cave has been found to contain a rich invertebrate fauna in keeping with that observed in other areas of the state, and this diversity is due, at least in part, to the wide variety of substrates and consequently habitat types within the cave. Through the minimal impact nature of our program, these animals and habitat types have been able to be studied in an essentially undisturbed state, and this approach has yielded much valuable information. The species presented as examples in this paper are present in large numbers in Little Trimmer, and much of the new information reported has come about as a direct result of the Little Trimmer program. The slow rate of cave biological processes means that long-term, intensive studies are essential for comprehending the ecology of cave organisms, and the nine month incubation period and apparent longevity of the Tasmanian Cave Spider in particular demonstrate how ideal an opportunity the Little Trimmer program presents.

In view of the success of the Little Trimmer study, we fully endorse the 'sampling with replacement' recommendations of Slaney and Weinstein (at this conference), and believe that such low impact, non-collection studies are the way forward in biospeleological research. We believe that the Little Trimmer program is an excellent example of how data collection can be optimised yet at the same time balanced against the needs of faunal conservation.

Acknowledgements

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References

- Barr, T.C., 1968. Cave ecology and the evolution of troglobites. *Evolutionary Biology* 2: 35–102.
- Clarke, A., 1989. *Fauna from the caves and karsts of the Bubs Hill area, Western Tasmania*. From a report

- to the Department of Parks, Wildlife & Heritage, Tasmania. 24pp.
- Davey, A.G. and White, S., 1986. *Management of Victorian caves and karst*. A report to the Caves Classification Committee, Dept. of Conservation, Forests and Lands, Victoria.
- Eberhard, S.M., 1987. Notes on cave fauna. Pp. 24–30 in: Greenslade, P. (ed.), *Significance of the invertebrate faunas of the LEMONTHYME and Southern Forests*. Consultancy report to the Commonwealth Commission of Inquiry into the LEMONTHYME and Southern Forests, Tasmania.
- Eberhard, S.M., 1989. *Survey of cave fauna in the Western Tasmania World Heritage Area, Part III*. A report to the Department of Parks, Wildlife and Heritage, Tasmania. 18pp.
- Eberhard, S.M., 1990a. *Ida Bay karst study: the cave fauna at Ida Bay in Tasmania and the effect of quarry operations*. Report to the Department of Parks, Wildlife and Heritage, Tasmania. 25pp.
- Eberhard, S.M., 1990b. Biological resources. Pp.25–33 in: Spate, A. (ed.), *Kubla Khan Cave State Reserve, Mole Creek, Tasmania: draft pilot management study*.
- Eberhard, S.M., Richardson, A.M.M. and Swain, R., 1991. *The invertebrate cave fauna of Tasmania*. National Estate Grants Program. 174pp.
- Goede, A., 1967. Tasmanian cave fauna: character and distribution. *Helictite* 5: 71–86.
- Houshold, I. and Clarke, A., 1988. *Bubs Hill karst area resource inventory and management recommendations — with supplementary reports on the Surprise River, Cardigan River, Cheyne Range and Nelson Valley karst areas*. Unpublished report to the Department of Lands, Parks and Wildlife, Tasmania. 67pp.
- Howarth, F.G., 1983. Ecology of cave arthropods. *Annual Review of Entomology* 28: 365–389.
- Jasinska, E.J., and Knott, B., 1991. The importance of caves at Yanchep, Western Australia. Pp.55–57 in: *Proceedings of the 18th Biennial Conference of the Australian Speleological Federation Inc., Margaret River, Western Australia*. Australian Speleological Federation Inc.
- Knott, B., 1983. Amphipods from Nurina Cave — Nullarbor Plain. *ASF Newsletter* 101: 3–4.
- Marples, B.J., 1968. The hypochilomorph spiders. *Proceedings of the Linnean Society of London* 179: 11–31.
- Richards, A.M., 1971a. The Raphidophoridae (Orthoptera) of Australia, part 9. The distribution and possible origin of Tasmanian Raphidophoridae, with descriptions of two new species. *Pacific Insects* 13: 575–587.
- Richards, A.M., 1971b. An ecological study of the cavernicolous fauna of the Nullarbor Plain, Southern Australia. *Journal of Zoology* 164: 1–60.
- Richards, A.M. and Ollier, C.D., 1976. *Investigation and report on the ecological protection of Exit Cave near Ida Bay in Tasmania (for the National Parks and Wildlife Service, Tasmania)*. Unisearch Ltd., Sydney. 73pp.
- Richardson, A.M.M., Doran, N.E., Eberhard, S.M. and Swain, R. (in press). Bioconservation and Tasmanian Cave Fauna. *Papers and Proceedings of the Australasian Cave and Karst Management Association (ACKMA) Conference on Management of Caves and Karst, Gowrie Park, Tasmania* (May 1995).
- Smith, G., 1982. Cave fauna. Pp. 173–178 in: Dyson, H.J., Ellis R. and James, J.M. (eds), *Wombeyan Caves*. Sydney Speleological Society Occasional Paper No. 8.
- Vandel, A., 1965. *Biospeleology: the biology of cavernicolous animals* (translated from French by B.E. Freeman). Pergamon Press: Oxford, 524 pp.
- Wellings, G., 1977. Invertebrate fauna of Bungonia Caves. Pp 150–153 in: Ellis, R., Hawkins, L., Hawkins, R., James, J., Middleton, G., Nurse, B. and Wellings, G. (eds), *Bungonia Caves*. Speleological Society Occasional Paper No. 4, Sydney.

ANTS, DISTURBANCE AND REGENERATION IN EUCALYPT FORESTS

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Abstract

Hosking, A.C. and Turner, V., 1997. Ants, disturbance and regeneration in eucalypt forests. *Memoirs of the Museum of Victoria* 56(2): 655–657.

In a pilot study, the activity of the seed-eating ant *Prolasius pallidus* increased following disturbance in *Eucalyptus regnans* forests. Seed removal experiments in *E. regnans* and *E. obliqua* forests indicate that seed-eating ants may have a significant impact on the success of forest regeneration.

Introduction

In Australia, many forest types are logged for timber, burnt and subsequently sown to revegetate the area. An example is the Mountain Ash (*Eucalyptus regnans*) forests which are logged primarily in the Otway Ranges and Central Highlands of Victoria. The disturbance caused by logging and subsequent burning may significantly affect the community structure of flora and fauna, including ants.

Ants world-wide may have important impacts on plants, both as seed dispersers and as seed predators (Andersen and Yen, 1985; O'Dowd and Gill, 1984). The ant fauna of Australia is exceptionally diverse and abundant. Of the 2000 or so species of ants in Australia few are seed harvesters (Campbell, 1982). *Melophorus*, *Meranoplus*, *Pheidole*, *Monomorium* and some *Rhytidoponera* species represent the majority of Australian seed-eating taxa. However, ants are probably the most important post-dispersal seed predators in Australian forests and their activity may have important consequences for regeneration of plants.

Few studies have examined the effect of logging and subsequent burning of forests on ants or on seed removal rates (Neumann, 1991). To address this issue we have commenced a study in which we are asking two major questions:

1. Does logging and fire affect the species richness and abundance of ants?
2. After disturbance, what effect do ants have on forest regeneration using seed broadcasting?

Does disturbance affect ants?

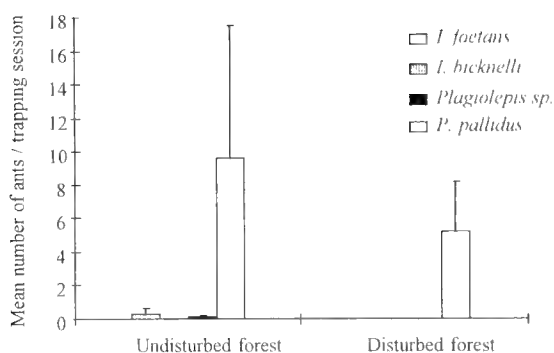
In a pilot study, we examined the abundance and species richness of ants in undisturbed *Eucalyptus*

regnans forests and at adjacent logged and burnt sites in the Central Highlands, Victoria.

Ten pitfall traps 2 cm in diameter were placed in two undisturbed *E. regnans* forests, two logged and burnt coupes and, at one site which was revegetated with *E. regnans* seeds three years previously. Pitfall traps were sampled after seven days, once during each season over one year at each site. *Prolasius pallidus*, a seed-eating ant, was the most abundant ant both at undisturbed and disturbed sites. *Iridomyrmex foetans* was present only at undisturbed sites, and *I. bicknelli* was present only at the revegetated site (Fig. 1). These preliminary results suggest that logging and burning affect the ant species composition and that species richness decreases with disturbance. Species richness of ants was particularly low, in contrast to other studies in different sites in the *E. regnans* forests of the Central Highlands (Neumann, 1992). Furthermore, ants were active throughout the year, and their species richness and relative abundance did not vary considerably from the data presented for Spring 1994.

We are currently conducting a more intensive survey of the effect of logging and fire on ant species richness and abundance. The study includes three *E. regnans* sites which were logged during Summer 1995–1996 and burnt in Feb 1996. At each site 20 pitfall traps placed along a 50 m transect are collected weekly and ant contents recorded. The mean number of ants for each species trapped at these sites will be compared to those from adjacent undisturbed plots both before and after logging, and after fire. So far, *P. pallidus*, is the most abundant ant trapped at each undisturbed site, however, the activity of this ant has increased after logging and post-fire to date, at each site. Also, ant species richness has declined from six species

A)



B)

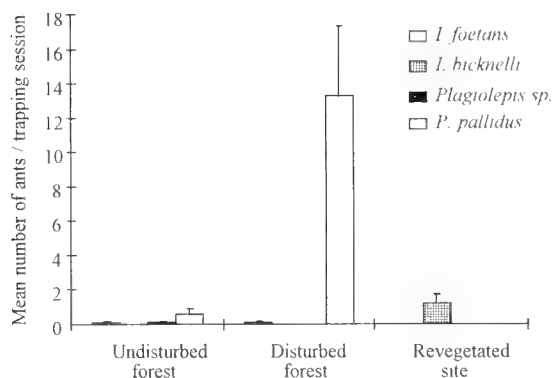


Figure 1. Mean number of ants trapped in pitfalls over 7 days ($n=10$, \pm SE), at A, site 1 in undisturbed and disturbed Mountain Ash forests and, at B, site 2, in undisturbed, disturbed and revegetated Mountain Ash forest during Spring 1994.

regularly trapped in undisturbed forest to two species; *P. flavicornis* and *P. pallidus*. *Prolasius pallidus* is believed to be an important seed predator in Mountain Ash forests in Victoria (Neumann, 1992).

What effect do ants have on forest regeneration?

Many studies have shown that the abundance of ants increases following fire. This increase in ant activity after a major habitat disturbance such as logging and fire may affect foraging rates on seeds. Seed-eating ants may have a particularly important impact on regeneration in areas which are being reafforested using broadcast seeds. In forests that are logged for timber and then burnt, seeds are sown directly onto the soil surface where they are available to ants.

Australian forestry services have used a variety of techniques to reduce seed removal or consumption by ants. Methods have included spraying insecticides in logged areas and their incorporation into clay pellets with seeds. Seeds have also been pelleted with clay to increase sowing accuracy of aerially broadcast seed.

In pilot studies, we examined whether seeds were removed by ants in *E. obliqua* and *E. regnans* forests and determined whether differences in removal rates occurred between pelleted and untreated seeds. Five replicates, each of ten pelleted and untreated seeds were placed onto perspex trays and covered with plastic coated wire umbrellas to protect seeds from rain. Significantly more pelleted *E. obliqua* seeds were removed than untreated seeds (Fig. 2). This may be explained by the high sugar content of the mucilage used to coat the clay to the seeds which may attract seed-eating ants.

However, when this experiment was repeated in a *E. regnans* forest the results were variable (Fig. 3). Slightly more pelleted and unpelleted seeds were removed from disturbed sites compared to undisturbed sites. Unseasonably poor weather conditions may have affected the

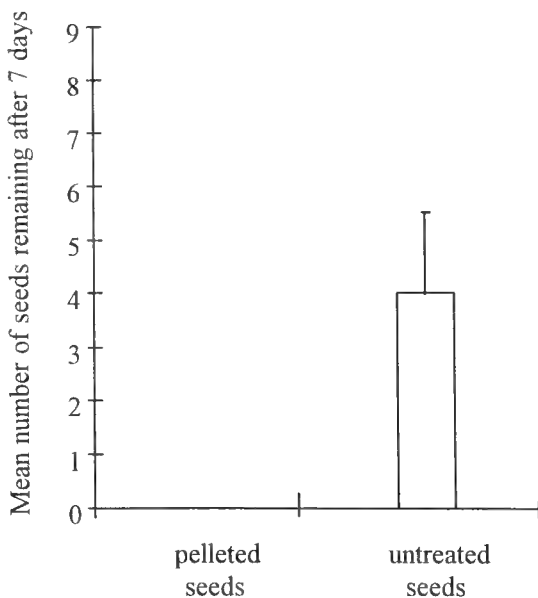


Figure 2. Mean number of pelleted and untreated *E. obliqua* seeds (\pm SE) remaining after 7 days in a Mess-mate forest. Significantly more pelleted seeds were removed compared to untreated seeds ($F_{1,28} = 19.7$, $P = 0.001$).

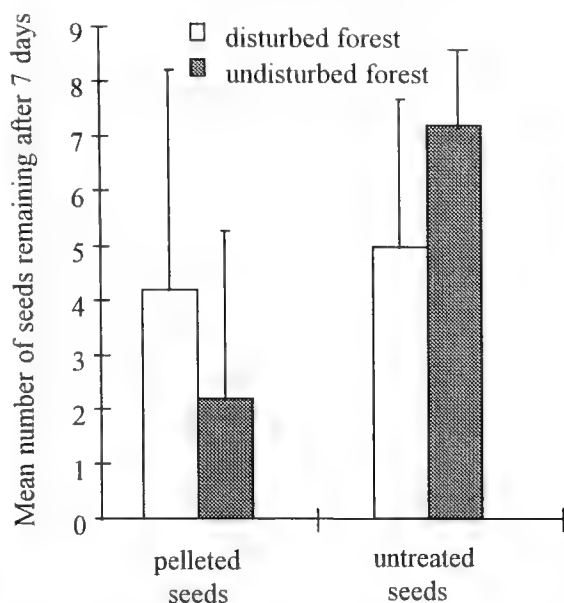


Figure 3. Mean number of pelleted and untreated *E. regnans* seeds (\pm SE) remaining after 7 days in a Mountain Ash forest.

results. If ants are attracted to pelleted seeds in other eucalypt forest types, this may have important implications for Australian forestry practices.

Further research

Logging, burning and subsequent seed broadcasting is commonly practiced by foresters in Australia. The effect this has on the removal rates of *E. regnans* seeds by ants in the Victorian Central Highlands will be examined. The main questions are:

1. After a forest is logged and burnt, do ants remove *E. regnans* seeds which are sown to revegetate the site?
2. *Prolasius pallidus* is the most abundant ant at each study site. This species is believed to be a seed-eating ant. If this species is active after major habitat disturbances, does it eat or remove broadcast seeds?
3. How is seed removal affected by different seed treatments (pelleted and untreated seeds) which are used in forestry practices?
4. Ants usually remove seeds from the soil surface. Covering seeds with a thin layer of soil may reduce access by seed-eating ants, thereby reducing seed removal rates. In addition, a thin layer of soil may actually

facilitate *E. regnans* seed germination. The effect of soil depth on removal germination of *E. regnans* seeds will be examined at logged, burnt sites and in the laboratory. This technique may lead to an increase in seed survival and germination success.

Summary

In Australian forests, ants are very diverse and abundant, and are considered the most important post-dispersal seed predators. Major habitat disturbances lead to an increase in surface activity which may consequently lead to an increase in seed removal rates.

Pilot studies have shown that ant abundances are affected to some degree by logging and fire, and that seeds are removed from logged and burnt sites. However, both activity and foraging rates are highly variable. Further studies will examine how disturbance affects ants, both before and after logging, and after fire.

So far, the potential impact of ants on regeneration success of eucalypts on logged and burned sites is unknown. However, the effects of ants on revegetation of logged areas may have important implications for future forest regeneration techniques used throughout Australia.

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References

- Andersen, A.N. and Yen, A.L., 1985. Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. *Australian Journal of Ecology* 10: 25-30.
- Campbell, M.H., 1982. Restricting losses of aerially sown seed due to seed-harvesting ants. Chapter 4 in: Buckley, R.C. (ed.), *Ant-plant interactions in Australia*. Dr. Junk Publishers: The Hague.
- Neumann, F.G., 1991. Responses of litter arthropods to major natural or artificial ecological disturbances in mountain ash forest. *Australian Journal of Ecology* 16: 19-32.
- Neumann, F.G., 1992. Responses of foraging ant populations to high-intensity wildfire, salvage logging and natural regeneration processes in *Eucalyptus regnans* regrowth forest of the Victorian Central Highlands. *Australian Forestry* 55: 29-38.
- O'Dowd, D.J. and Gill, M.A., 1984. Predator satiation and site alteration following fire: mass reproduction of Alpine Ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology* 5(4): 1052-1066.

BIODIVERSITY OF NEW ZEALAND BEETLES (INSECTA, COLEOPTERA)

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Abstract

Klimaszewski, J., 1997. Biodiversity of New Zealand beetles (Insecta: Coleoptera). *Memoirs of the Museum of Victoria* 56(2): 659–666.

Approximately 5235 species are described for New Zealand, including 354 introduced. They belong to 82 families in two suborders, Adephaga and Polyphaga. The New Zealand beetle fauna is distinguished by the absence of many major lineages, a high level of endemism, which in many groups is over 90% at the specific level and over 43% at the generic level (e.g., Staphylinidae), and the radiation of many groups of genera and species. The origins of New Zealand's beetle fauna are still poorly understood. They are likely to be varied, including Gondwanan elements and elements which arrived here by short and long-distance dispersal recently and in the remote past. The size of the New Zealand beetle fauna is consistent with species number/land area relationships in other areas around the world.

Introduction

The beetles are the largest order of organisms, with over 350 000 described species worldwide.

There are approximately 4881 described native and 354 introduced species of beetles in New Zealand (Appendix 1), representing c. 1094 genera in 82 families (Klimaszewski and Watt, in press). The total number of species is estimated at around 10 000 to 10 500 (Watt, 1976; Kuschel, 1990). In comparison, the vascular plant flora includes about 2500 species, and the terrestrial vertebrate fauna about 350 species (Watt, 1976). Watt (1976) estimated at 20 000 the number of described and undescribed species of terrestrial and freshwater Arthropoda probably occurring in New Zealand.

New Zealand beetles belong to two suborders, Adephaga and Polyphaga. Archostemata and Myxophaga, present in Australia, are absent from New Zealand. Four families (Archeocryptidae, Gyrinidae, Lycidae, and Trogidae) are present only as introduced species. One, Chalcodryidae, is endemic. Eleven families are represented by more than 100 species: Curculionidae (1321), Staphylinidae including Pselaphinae (1021), Carabidae (445), Colydiidae (196), Cerambycidae (188), Scydmaenidae (165), Chrysomelidae (156), Scarabaeidae (144), Elateridae (135), Tenebrionidae (134), and Scirtidae (125). Some smaller families — Byrrhidae, Cleridae, Hydraenidae, Corticariidae (=Latridiidae), Leiodidae, Melandryidae, and Trogossitidae — are also well represented in New Zealand. The most comprehensive local survey of New

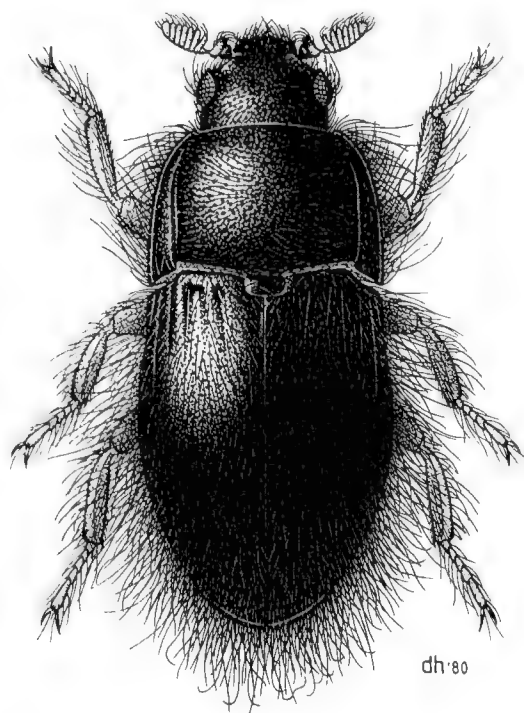
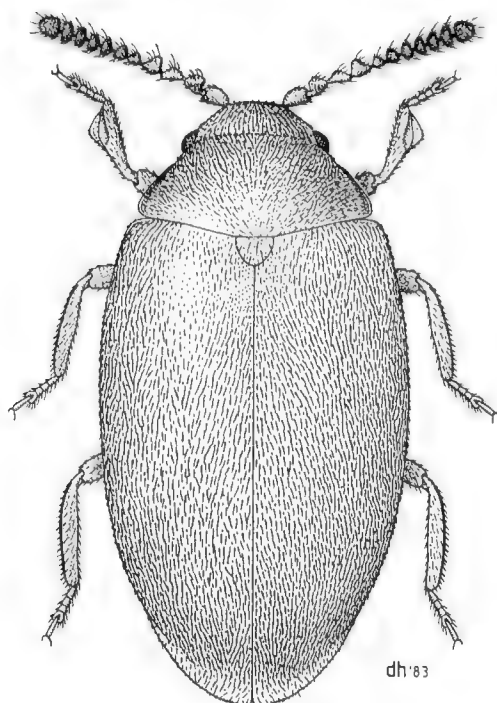
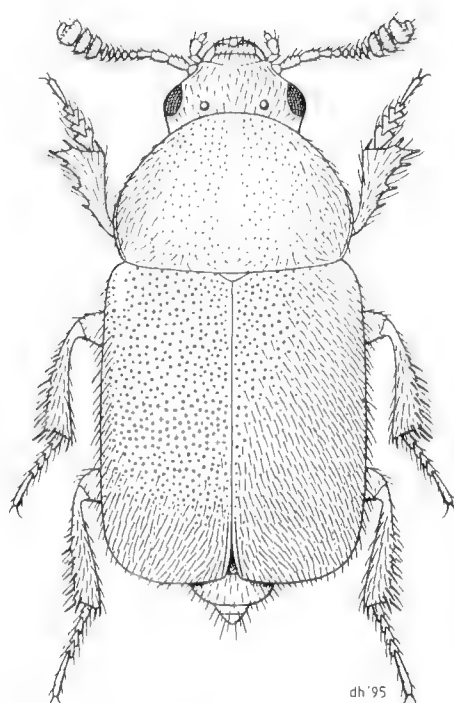
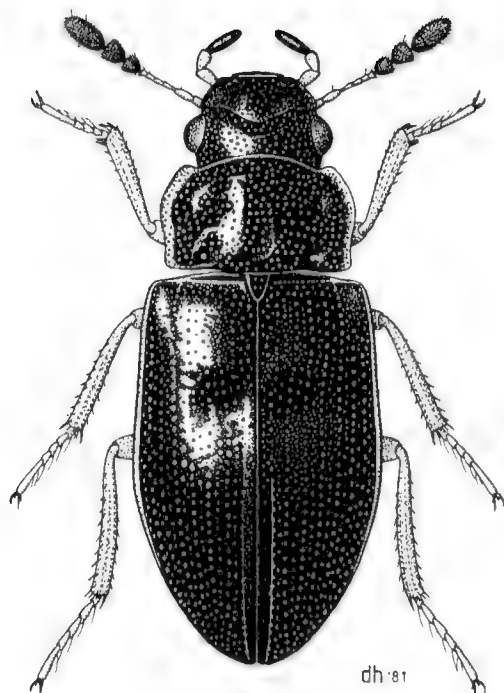
Zealand beetles is that of Kuschel (1990), in the suburb of Lynfield, Auckland, in which 982 beetle species were recorded in a diverse vegetation including remnant forest, pastureland, and suburban garden.

Factors responsible for the diversity and nature of the present-day New Zealand beetle fauna are:

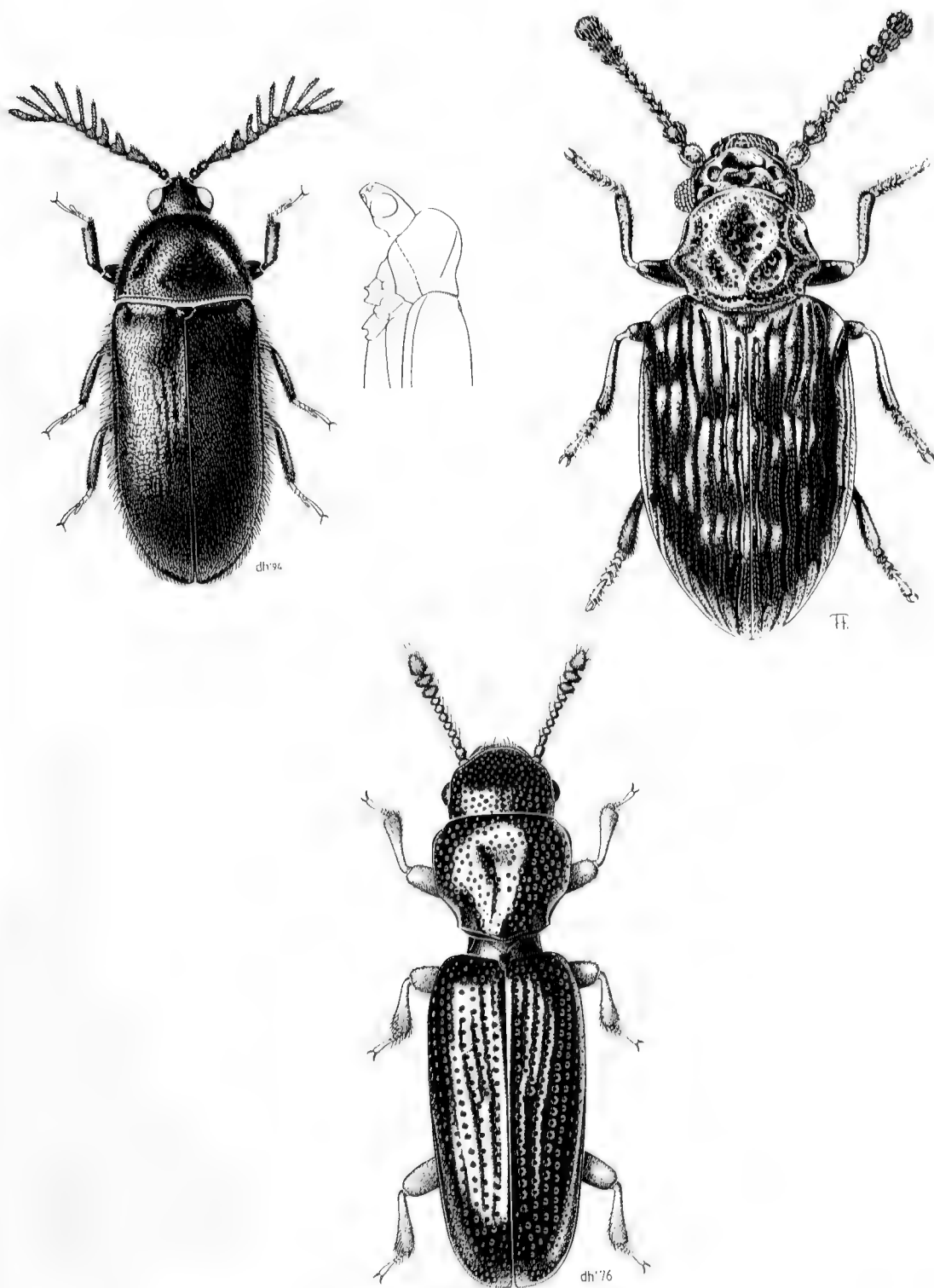
1. Gondwanan origin of some of our biota;
2. approximately 80 million years of geographic isolation of New Zealand, which has resulted in a high level of generic endemism and approximately 90% endemism at the specific level;
3. changing climate, changing shorelines (Oligocene bottleneck) (Cooper and Millner, 1993; Cooper and Cooper, 1995), orogenies, glaciation, and volcanic activity; and
4. absence of terrestrial mammals and other animals and plants which have dominated ecosystems elsewhere in the world.

Origin of New Zealand beetles

The New Zealand region and its ancestral biota originated in the fragmentation of part of an ancient supercontinent, Gondwana (Cooper and Millner, 1993; Cooper and Cooper, 1995). In the late Cretaceous c. 80–85 mya (million years ago), the New Zealand region had separated from the remainder of Gondwana through active sea-floor spreading and broadening of the Tasman Sea. The New Zealand region with its biota thus has been geographically isolated for approximately the last 80 mya, and during this period has undergone an active tectonic and



Figures 1–4. 1, *Horelophus walkeri* Orchymont, beetle of the endemic subfamily Horelophinae (Hydrophilidae); 2, *Microsilpha litorea* Broun, endemic species of Microsilphinae (Staphylinidae); 3, *Amplectopus pallicornis* Broun (Scirtidae); 4, *Parnida agrestis* Broun, endemic species (Dryopidae).



Figures 5–7. 5, *Brounia thoracica* Sharp, only New Zealand member of Chelonariidae; 6, *Nothoderodontus gourlayi* Crowson (Derodontidae); 7, *Saphophagus minutus* Sharp (Jacobsoniidae).

volcanic history. These events have had profound effects on the composition and distribution of plants and animals, including beetles, and influenced their evolution. Certainly some of the contemporary New Zealand beetles have evolved from ancient Gondwanan forms. The modern beetle fauna consists of ancient, variously changed lineages, elements introduced by dispersal over short and long distance (e.g., groups dispersed passively over water as a result of the strong westerly winds and currents around the 40th parallel), and species intentionally and accidentally introduced. The fauna was greatly influenced in the last 1000 years by people who brought devastation to native forest and introduced harmful exotic animals — possum, rats, goats, deer and others (Ramsay, 1978).

Support of the hypothesis that many of our beetles are of ancient origin comes from the high endemism, over 90% at the specific level, with several endemic subfamilies and tribes and many endemic genera (Watt, 1982). Several usually small families are represented in New Zealand by diverse endemic forms (e.g., Byrrhidae, Colydiidae, Hydraenidae, Melandryidae, Ptiliidae, Scirtidae and Scydmaenidae). Native species are those primarily associated with the lowland forest which has prevailed throughout most of New Zealand's geological history, the alpine habitats, the tussock grasslands, and the subantarctic islands (Kuschel, 1990). Introduced species are mostly associated with anthropogenic habitats (Kuschel, 1990). Many groups' distribution patterns are suggestive of a Gondwanan or pre-Gondwanan origin: for instance, the remnant relict genera of tenebrionoid Pilipalpinae persisting in Madagascar, New Zealand, southern South America, and Australia. The Nosodendridae occur in New Zealand, Australia, southern Africa, Madagascar, and the Holarctic region. The staphylinid *Stylogymnusa subantarctica* Hammond is known only from the Auckland Islands, with its closest relatives exclusively Holarctic. The New Zealand jacobsoniid beetle *Saphophagus minutus* Sharp was considered by Crowson (1959) as a relict coeval with the tuatara. The Chaetosomatidae are known only from New Zealand and Madagascar, and the Phycosecidae only from New Zealand and Australia. The small family Cavognathidae, with species occurring in birds' nests, are also known only from New Zealand and Australia. The New Zealand Nemonychidae are closest to species from Chile. Omaliine staphylinids of the genus *Metacorneolabium* (22 species) are distributed in New Zealand, Aus-

tralia, and South America. Some southern temperate Staphylinidae from families Hydraenidae, Ptiliidae, Agryrtidae, Leioldidae, Pselaphidae, and Staphylinidae show 'transaustral disjunctions' (occur on two or more widely separated southern land areas) — New Zealand, Australia, South Africa, and/or South America.

Comparison of Staphylinidae in New Zealand and other areas

The family Staphylinidae in New Zealand includes approximately 936 native and 85 adventive species (Klimaszewski et al., 1996). A comparison of the estimated numbers of species of rove beetles in New Zealand, the Hawaiian Islands, Florida, the British Isles, Central Europe, Fennoscandia, Australia, and North America north of Mexico is presented in Table 1. Species numbers are the result of many factors besides land area, including latitude, climate, topography (resulting in habitat diversity), and the geological and biological history of an area (including the impact of Pleistocene glaciations and the degree and duration of isolation from other areas).

New Zealand's staphylinid fauna is comparable in size, in relation to land area, to the faunas of a diversity of areas. This is quite striking in view of New Zealand's much longer isolation from other lands (compared to the other areas in Table 1) and its perhaps consequent lack of several major lineages of Staphylinidae. The tremendous topographic, climatic, and vegetational diversity of New Zealand is likely to have enhanced speciation. There could also be a connection between the absence of several lineages and the extensive New Zealand radiations in *Microsilpha*, *Sagola*, **Euplectopsis*, *Eupines*, *Sepedophilus*, *Oligota*, **Paratorchus*, *Hypromma*, *Othius*, and *'Quedius'* [*endemic genera]. Far more knowledge of the ecological roles of staphylinid groups both in New Zealand and elsewhere is needed however, to test such an hypothesis.

The origins of New Zealand's staphylinid fauna are still poorly understood. They are probably varied, since the fauna includes over 20 genera or higher groups shared only with other southern temperate regions (Newton, 1985), as well as numerous more widespread lineages (e.g., *Sepedophilus*, *Gyrophaena*, *Oligota*, *Mylaelaena*, *Polylobus*, *Bledius*, *Carpelimus*, *Oxytelus*, *Lathrobiina sensu lato*, *Othius*, *Quediina*, *Cafius*, and *Philonthus*). Phylogenetic studies of all lineages within and outside New Zealand are

Table 1. Comparison of land areas and estimated numbers of species of Staphylinidae (including Pselaphinae, Scaphidiinae, Dasycterinae, and other groups) for several parts of the world (Klimaszewski, 1996).

Zoogeographical area	Land area (km ²)	Estimated species	Source of estimate
USA.: Hawaiian Islands	16 700	100	Nishida (1994)
USA.: Florida	140 800	498	Peck and Thomas, unpublished checklist
New Zealand	268 800	936	Newton and Thayer (1995), unpublished checklist; Chandler (1991), (Pselaphinae)
British Isles	315 000	1046	Pope (1977)
Central Europe (Austria, Czech Republic, Germany, Poland, Slovakia)	882 250	1949	Lucht (1987); Lohse and Lucht (1989)
Fennoscandia (Finland, Norway, Sweden)	1 073 500	1222	Silfverberg (1992)
Australia	7 692 300	2441	Newton & Thayer (1995), unpublished checklist; Chandler, in litt. (Pselaphinae)
North America (N of Mexico)	19 115 250	3974	Arnett (1985); Chandler (1994), (Pselaphinae)

needed in order to understand the history of the New Zealand staphylinid fauna.

Estimated number of species for Australia and New Zealand includes known described and undescribed species, but excludes adventive species. Adventive species are also excluded from the Hawaiian Islands number, but not from the other geographic areas, where the number of adventive species is not known, but probably very low. Known but undescribed species are also included for Florida, but not for the remaining areas, where the number is not known, but probably low.

Acknowledgements

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References

- Arnett, R.H., 1985. *American insects. A handbook of the insects of America north of Mexico*. Gainesville, Flora and Fauna Publications. 850 pp.
- Chandler, D.S., 1991 and 1994. *Unpublished checklist of Pselaphinae (Staphylinidae)*.
- Cooper, A. and Cooper, R.A., 1995. The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society of London B* 261: 293–302.
- Cooper, R.A. and Millner, P.R., 1993. The New Zealand biota: historical background and new research. *Trends in ecology and evolution* 8: 429–433.
- Crowson, R.A., 1959. Studies on the Dermestoidea (Coleoptera), with special reference to the New Zealand fauna. *Transactions of the Royal Entomological Society of London* 3(4): 81–94.
- Klimaszewski, J. and Watt, J. C., in press. Beetles of New Zealand: family-group review and keys to identification (Insecta: Coleoptera). *Fauna of New Zealand*.
- Klimaszewski, J., Newton, A.F. and Thayer, M., 1996. A review of the New Zealand rove beetles (Coleoptera: Staphylinidae). *New Zealand Journal of Zoology* 23: 143–160.
- Kuschel, G., 1990. Beetles in a suburban environment: a New Zealand case study. *DSIR Plant Protection Report* 3. 119 pp.
- Lawrence, J.F., and Newton, A.F., 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). Pp. 779–1006 in: Pakaluk, J. and Slipinski, S.A. (eds), *Biology, phylogeny, and*

- classification of Coleoptera: papers celebrating the 80th birthday of Roy Crowson*. Muzeum i Instytut Zoologii PAN: Warsaw.
- Lohse, G.A. and Lucht, W.H., 1989. *Die Käfer Mitteleuropas; 1. Supplementband mit Katalogteil*. Goecke and Evers: Krefeld. 346 pp.
- Lucht, W.H., 1987. *Die Käfer Mitteleuropas; Katalog*. Goecke and Evers: Krefeld. 342 pp.
- Newton, A.F., 1985. South temperate Staphylinioidea (Coleoptera): their potential for biogeographic analysis of austral disjunctions. Pp. 180–220 in: Ball, G.E. (ed.), *Taxonomy, phylogeny and zoogeography of beetles and ants*. Dr W. Junk Publishers: Dordrecht.
- Newton, A.F. and Thayer, M.K., 1995. Protopselaphinae new subfamily for *Protopselaphus* new genus from Malaysia, with a phylogenetic analysis and review of the Omaliinae group of Staphylinidae including Pselaphidae (Coleoptera). Pp. 219–320 in: Pakaluk, J. and Slipinski, S.A. (ed.), *Biology, phylogeny and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson*. Muzeum i Instytut Zoologii PAN: Warsaw.
- Nishida, G.M. (ed.), 1994. Hawaiian terrestrial arthropod checklist, second edition. *Bishop Museum Technical Report 4*. iv + 287 pp.
- Peck, S.B. and Thomas, M.C. (unpublished). *A list of Coleoptera of Florida*.
- Pope, R.D., 1977. Coleoptera and Strepsiptera. In: Kloet, G.S. and Hincks, W.D. (eds), *A check list of British insects (second edition)*. Handbooks for identification of British Insects 11(3). Royal Entomological Society of London: London. xiv + 105 pp.
- Ramsay, G.W., 1978. A review of the effect of rodents on the New Zealand invertebrate fauna. *New Zealand Lands and Survey Department, Information Series 4*: 89–97.
- Silfverberg, H., 1992. *Enumeratio Coleopterorum Fennoscandiae, Daniae et Baltiae*. Helsingin Hyönteisvaihtoyhdistys: Helsinki. v + 94 pp.
- Watt, J.C., 1976. A biological survey in New Zealand. *The New Zealand Entomologist* 6(2): 138–143.
- Watt, J.C., 1982. 1981 Presidential address: New Zealand and beetles. *The New Zealand Entomologist* 7(3): 213–221.

Appendix 1 Inventory of New Zealand beetles. Classification adopted from Lawrence and Newton (1995). Suborders and families with over hundred species are in bold.

Taxon	Approximate number of recorded native species	Approximate number of introduced and adventive species
Suborder ADEPHAGA		
Superfamily CARABOIDEA		
1. Rhysodidae	6	0
2. Carabidae (including Cicindelinae)	426	19
3. Dytiscidae	12	1
4. Gyrinidae	1	1
Suborder POLYPHAGA		
Series STAPHYLINIFORMIA		
Superfamily HYDROPHILOIDEA		
5. Hydrophilidae	70	5
6. Histeridae	22	6
Superfamily STAPHYLINOIDEA		
7. Hydraenidae	32	0
8. Ptiliidae	48	8–9
9. Agyrtidae	2	0
10. Leiodidae	112	1
11. Scydmaenidae	201	1
12. Staphylinidae	936	85
Series SCIRTIFORMIA		
Superfamily SCIRTOIDEA		
13. Scirtidae	125	0
14. Eucinetidae	1	0
15. Clambidae	8	2

Appendix 1 Continued.

Taxon	Approximate number of recorded native species	Approximate number of introduced and adventive species
Series SCARABAEIFORMIA		
Superfamily SCARABAEOIDEA		
16. Lucanidae	24	4
17. Trogidae	0	1
18. Scarabaeidae	132	12
Series ELATERIFORMIA		
Superfamily BUPRESTOIDEA		
19. Buprestidae	3	1
Superfamily BYRRHOIDEA		
20. Byrrhidae	79	0
21. Dryopidae	4	0
22. Elmidae	16	0
23. Limnichidae	7	1
24. Heteroceridae	1	0
25. Ptilodactylidae	6-8	0
26. Chelonariidae	1	0
Superfamily ELATEROIDEA		
27. Eucnemidae	22	0
28. Elaterridae	132	3
29. Lycidae	0	1
30. Cantharidae	40	1
Series BOSTRICHIFORMIA		
Superfamily DERODONTOIDEA		
31. Derodontidae	1	0
Superfamily BOSTRICHCHOIDEA		
32. Jacobsoniidae	3	0
33. Nosodendridae	2	0
34. Dermestidae	11	6
35. Bostrichidae (incl. Lyctinae)	1	7
36. Anobiidae (incl. Ptininae)	28	11
Series CUCUJIFORMIA		
Superfamily CLEROIDEA		
37. Trogossitidae	24	1
38. Chaetosomatidae	4	0
39. Cleridae	37	2
40. Phycosecidae	1	0
41. Dasytidae	33	0
Superfamily CUCUJOIDEA		
42. Nitidulidae	21	11
43. Monotomidae	1	5
44. Phlocostichidae	2	0
45. Silvanidae	7	5
46. Cucujidae	1	0
47. Laemophloidae	3	3
48. Phalacridae	3	1
49. Cavognathidae	5	0
50. Cryptophagidae	23	12
51. Languridae	8	0
52. Erotylidae	9	0
53. Bothrideridae	6	1

Appendix 1 Continued.

Taxon	Approximate number of recorded native species	Approximate number of introduced and adventive species
54. Cerylonidae	5	0
55. Endomychidae	6	1
56. Coccinellidae	22	18
57. Corylophidae	19	2
58. Corticariidae (= Lathridiidae)	53	11
Superfamily TENEBRIONOIDEA		
59. Mycetophagidae	12	1
60. Archeocrypticidae	0	1
61. Ciidae	20	0
62. Melandryidae	38	0
63. Mordellidae	6	1
64. Rhipiphoridae	5	0
65. Colydiidae	196	0
66. Ulodidae	20	0
67. Chalcodryidae	5	0
68. Tenebrionidae	149	10
69. Prostomidae	1	0
70. Oedemeridae	18	3
71. Pyrochroidae	7	0
72. Salpingidae	22	0
73. Anthicidae	17	9
74. Aderidae	15	0
75. Scraptidae	4	0
Superfamily CHRYSOMELOIDEA		
76. Cerambycidae	180	8
77. Chrysomelidae	134	19
Superfamily CURCULIONOIDEA		
78. Nemonychidae	4	0
79. Anthribidae	58	3
80. Belidae	11	0
81. Brentidae	3	1
82. Curculionidae	1496	46

AUSTRALIA'S MOST DIVERSE CRAYFISH HABITAT?

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Abstract

Morey, J. and Hollis, G., 1997. Australia's most diverse crayfish habitat? *Memoirs of the Museum of Victoria* 56(2): 667–669.

Labertouche Creek, a tributary of the Tarago River in West Gippsland, arguably has the most diverse freshwater crayfish assemblage in Australia. Six crayfish species are known from the creek, including the rare and vulnerable Warragul Burrowing Crayfish, *Engaeus sternalis*, the only known location of this species in Australia (Horwitz, 1990, 1992). Other species of burrowing crayfish found are *E. hemicirratulus*, *E. cunicularius*, and *E. quadrimanus*. Two species of *Euastacus* (Spiny Freshwater Crayfish) are also known from these waters, *Euastacus yarraensis* and *E. kershawi* (Gippsland Spiny Crayfish). A third species, *E. woiwuru*, is possibly present, as the creek is shown to be within this species' range.

Introduction

Labertouche Creek, a tributary of the Tarago River in West Gippsland, possibly has Australia's most diverse freshwater crayfish assemblage, with six species of freshwater crayfish (four species of burrowing crayfish of the genus *Engaeus* (Decapoda: Parastacidae) and two spiny crayfish of the genus *Euastacus* (Decapoda: Parastacidae) known to be present and a seventh species (*E. woiwuru*) suspected of being present, as the creek is within its range (Morgan, 1986). Adult burrowing crayfish are generally small, total length rarely exceeding 100 mm, whereas the adult spiny crayfish are considerably larger than 100 mm in total length.

A survey was conducted to confirm the presence of the Warragul Burrowing Crayfish, *Engaeus sternalis* (Clark), and determine the suitability of pitfall trapping as a survey technique for the species. *E. sternalis* has been classified as Endangered by the Department of Conservation and Natural Resources on the basis of its single confirmed location and as a 'taxa in danger of extinction in Victoria and whose survival is unlikely if the factors causing their decline continue operating' (CNR, 1993, IUCN, 1983). The species was listed under the Flora and Fauna Guarantee Act 1988 in March 1993 (SAC, 1993).

Specimens were collected in pit fall traps adjacent to the creek following heavy spring rain during this survey. Three pitfall lines, consisting of between 6 and 41 traps, constructed from 90 mm PVC tubing cut into 200 mm lengths, (with tin lids in the bottom), were established in grazing land adjacent to Labertouche Creek, 50 m downstream from the 1982 collection site of *E.*

sternalis (Horwitz, pers comm). The pitfall traps were distributed at approximately 0.5 m intervals at a number of different locations at the study site to determine whether *E. sternalis* utilises different areas along the creek. This included pitfall traps located along the bank of the creek (<1 m to edge), perpendicular to the creek (approx 10 m) and in the banks of the creek. Several traps installed in the banks of the creek were lost during floods. Trapping commenced on 26 Jun 1995 and continues to the present. A 200 mm high driftfence was erected between pitfall traps to act as a superficial barrier directing greater numbers into the pits than would otherwise occur. This driftfence however, was removed on 31 Jul 1995 due to the presence of cattle at the study site. Pitfall traps were checked mostly at 2–5 day intervals.

Results of pitfall trapping to mid-November are summarised in Table 1. No crayfish were caught in traps between 26 June and 8 August. All species were collected from September onwards, usually after rainfall, however *E. sternalis* was only captured after rainfall. *E. sternalis* and *E. cunicularius* have so far only been collected within 0.5 m to the creek bank, whereas *E. quadrimanus* and *E. hemicirratulus* were recorded along the bank and up to 8 m perpendicular to the bank within the cleared grazing area. The number of adults collected was almost the same as the number of juveniles (14 adults, 15 juveniles), indicating both age classes responded equally to, or took advantage of, the wet weather to disperse on the surface. It is still not known how *E. sternalis* reaches the surface, as none of its tunnel systems so far investigated has come to the surface (Horwitz, 1990a).

Table 1. *Engaeus* species collected in pitfall traps adjacent to Labertouche Creek 26 Jul to 20 Nov 1995. F = Female, M = Male, u = Sex unknown, ad = adult, juv = juvenile, E quad/cunic = unable to identify.

Date	<i>E sternalis</i>	<i>E hemicirratulus</i>	<i>E quadrimanus</i>	<i>E cunicularius</i>	<i>E quad/cunic</i>
8 Aug			1u (ad)	1u (ad)	
13 Sep	1F (ad)	2u (juv)			
21 Sep		1u (juv)			
24 Sep				1M (ad)	
8 Oct		1u (juv)			
14 Oct			2u (ad)	1M, 1F (ad)	5u (juv)
21 Oct	1F (ad)	1u (juv)	1F (ad)		
23 Oct			1F (ad)	1M (ad)	
29 Oct		1u (ad)			
10 Nov	1u (juv)	1M (ad)	1u(juv?)		3u (juv)
Total	3	7	6	5	8

Species encountered

Engaeus sternalis. Despite extensive searching, the only known location in Australia of this species is on Labertouche Creek and prior to this survey, was found in complex burrow systems in clayey soils in the creek bank (Horwitz, 1990a, 1990b). Nothing is known about its biology or ecology. This species is easily identified by its pale yellow-grey colour, a covering of fine downy hairs on its carapace and dimorphic chelae, and very small eyes.

Engaeus hemicirratulus Smith and Schuster, is a common burrowing species easily identified by its bright orange claws, many stiff hairs and very short antennae. Their burrows typically have a fan shaped chimney, with tunnels descending obliquely to chambers which are occasionally just below the ground surface. Males and females are frequently found together in the same burrow and are usually accompanied by juveniles (Horwitz, 1990b). Burrows are typically in yellow-orange clay dominated soils, which was originally covered in dense wet forest. This species is common and widespread throughout its range in Gippsland, usually above an altitude of 100m.

Engaeus cunicularius (Erichson) is a common species, generally brown and with the top side of dactyl (the smaller movable part of the claw), slightly rough or granulated (Horwitz, 1990b). Often found in sympatry with *E quadrimanus*, and in similar habitat types (Horwitz, 1990b). It constructs burrows connected to the water table and/or to permanent water (Horwitz and

Richardson, 1986; Horwitz, 1990b). *E. cunicularius* is found from near the Otways in western Victoria throughout south eastern Victoria, the Bass Strait islands and Tasmania (Horwitz, 1990b).

Engaeus quadrimanus Clark, another common species, is very similar to *E. cunicularius* but the dactyl is smooth. These two can only be distinguished from each other as adults; if total length (tip of claws to tip of tail) is 50–60 mm. It is considered a lowland species and found in a range of vegetation types from ferny gullies to near rainforest, and in swamps and creeks (Horwitz, 1990b). *E. quadrimanus* constructs burrows, usually with more than one opening and often with conical, pelleted chimneys, down to the water table (Horwitz, 1990b, Horwitz and Richardson, 1986). Distribution is from north of Melbourne to Mallacoota, near the Victoria–New South Wales border (Horwitz, 1990b).

Euastacus yarraensis (McCoy) is generally dark olive green with white and orange claws. The spines on the abdomen and some bumps on the carapace are orange with white tips/centres. Females mature at close to 40 mm Occipital Carapace Length, (the distance from the rear of the eye socket to the centre of the posterior of the carapace). Berried females have been collected in surveys in September through to November (Morgan, 1986). *E. yarraensis* is found from the Tarago River through to the Otways in south western Victoria.

Euastacus kershawi (Smith) (Gippsland Spiny Crayfish) is usually dark olive green, often with orange markings on the under-side, but with no white on the claws, and has sharp spines on the front legs and abdomen. It can grow large, although specimens over 120 mm carapace length are uncommon. Females are generally sexually mature at OCL greater than 85 mm, although some specimens appear to be sexually mature between 50 mm to 80 mm OCL (Morgan, 1986). Recent surveys by the first author indicate this species is very slow growing, averaging an annual increase of only 7 mm OCL. Specimens have occasionally been found many metres away from permanent water. Some individuals construct burrows of type 1b or 2 (Horwitz and Richardson, 1986), adjacent to river banks. Found from the Tarago River to almost the New South Wales border in southerly flowing rivers and streams.

A third species of this genus, *Euastacus woiwuru* Morgan is possibly present, as the creek is within the species' range, (Morgan, 1986) but as yet has not been recovered during surveys. It is similar in size to *E. yarraensis*, but relatively poorly spined (Morgan, 1986).

Prior to this survey, *E. sternalis* was only found by destructive sampling of the creek bank, however results show that pitfall trapping is a feasible alternative of survey for this cryptic species, as well as for some other species of burrowing crayfish. It appears that *E. sternalis*, along with other sympatric species, respond to rainfall and increasing ground temperature for above ground dispersal.

Preliminary results confirm Horwitz's opinion that *E. sternalis* is confined to the creek bank, although no doubt the species could be

found in adjacent damp areas with more extensive surveys. A community awareness program and site protection works are currently being undertaken to protect the habitat of *Engaeus sternalis*.

Acknowledgments

Permission from the landholder, Mr Barry Whiting, to survey on his property is greatly appreciated. The project was funded by a grant from the Australian Heritage Commission.

References

- CNR, 1993. *Threatened Fauna in Victoria*. Department of Conservation and Natural Resources: Melbourne.
- Horwitz, P., 1990a. The conservation status of Australian freshwater Crustacea. *Australian National Parks and Wildlife Service Report Series No 14*.
- Horwitz, P., 1990b. A taxonomic revision of species in the freshwater crayfish genus *Engaeus* Erichson (Decapoda: Parastacidae). *Invertebrate Taxonomy* 4: 427-614.
- Horwitz, P. H.J. and Richardson, A. M., 1986. An ecological classification of the burrows of Australian freshwater crayfish. *Australian Journal of Marine and Freshwater Research* 37: 237-242.
- IUCN, 1983. *The IUCN Invertebrate Red Data Book*. International Union for Conservation of Nature and Natural Resources, Switzerland.
- Morgan, G.J., 1986. Freshwater crayfish of the genus *Euastacus* Clark (Parastacidae) from Victoria. *Memoirs of the Museum of Victoria* 47: 1-57.
- SAC (Scientific Advisory Committee, Flora and Fauna Guarantee), 1993. *Final recommendation on a nomination for listing: Engaeus sternalis*. Department of Conservation and Natural Resources, Victoria.

ANT COMMUNITIES AS BIO-INDICATORS IN RELATION TO FIRE MANAGEMENT OF SPOTTED GUM (*EUCALYPTUS MACULATA* HOOK.) FORESTS IN SOUTH-EAST QUEENSLAND

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Abstract

Vanderwoude, C, Andersen, A.N. and House, A.P.N., 1997. Ant communities as bio-indicators in relation to fire management of spotted gum (*Eucalyptus maculata* Hook.) forests in south-east Queensland. *Memoirs of the Museum of Victoria* 56(2): 671–675.

As a pilot test of the potential for using ant communities as bio-indicators in forest monitoring programs, the effects of different fire regimes on ant community structure were studied at Bauple State Forest in 1994 and 1995. Three sites had been subjected to long-term burning regimes of: annual burning; periodic burning (2–3 years); and no burning. Two grids of pitfall traps were established in each compartment, and ants were sampled monthly between May 1994 and April 1995. A total of 88 species from 42 genera were recorded, with 74 species found from the annually burned site, 63 from the periodically burned site, and 43 from the unburned site. The relative abundance of Eyrean (arid) taxa was particularly high (36%), and that of Bassian (cool temperate) taxa low (8%) at the annually burned site, with the reverse true for the unburned site (14% and 20% respectively). Burning frequency also affected the dominance of functional groups. The relative abundance of Dominant Dolichoderinae (species of *Iridomyrmex*) was positively related to fire frequency, while Opportunists (mostly species of *Rhytidoponera*) comprised 65% of all ants at the unburned site, but only 16% at the annually burned site. These site differences conform to known ant-fire-habitat relationships elsewhere in Australia. We have not only shown that ant communities are sensitive to fire management practices in Bauple State Forest, but have demonstrated that an effective ant sampling program is a practicable option.

Introduction

There is increasing interest in the use of 'indicator' groups of invertebrates for assessing and monitoring ecological change associated with land management practices (Rosenberg et al., 1986; Noss, 1990; Spellerberg, 1993; Williams, 1993). In the context of forest management, a variety of major disturbances (including timber harvesting, fire and grazing) have the potential to be monitored using indicator groups. Such monitoring has traditionally focused on vascular plants and vertebrates, but there is growing acknowledgement that these taxa provide a limited view of the state of an ecosystem after disturbance. A more reliable indication of ecosystem health is likely to be provided by invertebrates (Rosenberg et al., 1986; Spellerberg, 1993; Williams, 1993), and the recent development of rapid biodiversity assessment techniques (Oliver and Beattie, 1993, 1996) makes invertebrates a realistic monitoring option.

Ants are ideal candidates for use as bio-

indicators in the Australian environment because:

1. they are highly abundant and diverse in most habitats;
2. they are functionally important at all trophic levels;
3. they can be sampled and sorted with relative ease;
4. species composition is highly sensitive to ecological change; and
5. species can be classified into functional groups which vary predictably in relation to environmental stress and disturbance (Majer, 1983; Greenslade and Greenslade, 1984; Andersen, 1990, 1995).

Ants have a long history of use as bio-indicators of restoration success following mining (Majer, 1983, 1984, 1985; Andersen 1993a), and more recently have been incorporated into forestry monitoring programs, especially in relation to fire (Neumann, 1992; York, 1994).

The Queensland Forestry Research Institute has recently established a pilot ant survey program as a basis for their potential use as indi-

cators of the ecological effects of forest management practices (Vanderwoude et al., submitted). Ants have been surveyed at sites subject to different burning regimes, and the differences in ant communities at these sites are reported here.

Methods

Study site

Our study was conducted in Bauple State Forest (25° 55'S, 152° 40'E), approximately 225 km N of Brisbane in south-east Queensland. The area is part of the humid subtropics (Brown and Turnbull, 1986). Mean annual rainfall is 1100 mm, with over 50% falling in the summer months between December and March.

Bauple State Forest consists mainly of open eucalypt forest with an understorey of *Acacia* species. Dominant canopy trees are *Eucalyptus maculata* Hook. and *Eucalyptus drepanophylla* F. Muell. ex Benth., while the main understorey trees are *Acacia aulacocarpa* Cunn. ex Benth. and *Acacia leiocalyx* (Domin) Pedley. *Alphitonia excelsa* (Cunn. ex Fenzl) Reissack ex Benth. and the introduced weed *Lantana camara* L. are also common in the understorey where the soils are deeper and more fertile.

Three sites within the forest had been subjected to experimental burning regimes as follows:

1. annually burned (314 ha) by spring fires since 1952;
2. periodically burned (423 ha) by spring fires every 2–3 years since 1973; and
3. unburned (296 ha) since at least 1946.

Annual and periodic burning have resulted in the development of a grassy ground layer and a reduction of woody understorey plants, while the absence of fire at the unburned site has resulted in a heavy litter layer and the establishment of a greater proportion of fire-sensitive understorey plants in favour of grasses (Henry, 1961; Henry and Florence, 1966; House, 1995).

Sampling

Ants were sampled by pitfall traps within two plots at each site. These were selected to capture within-site variation, and do not represent treatment replicates. Nine pitfall traps (18 mm o.d. test tubes inserted in permanent sleeves, following Majer, 1978) were established in each plot, as a 3 x 3 array with 5-m spacing. Preservative was 70% ethanol to which a small quantity of glycerol had been added. Digging-in effects (Greenslade, 1973) were minimised by establishing plots several weeks prior to opening the

trapps. Pitfalls were opened for seven days each month from May 1994 to April 1995.

Analysis

Ants were sorted to species, and species abundances in each trap were square-root transformed to avoid distortions caused by large numbers of individuals falling into a few traps (Southwood, 1978; Andersen, 1983, 1991). A species' total abundance was defined as the sum of transformed abundances from individual traps. Data from the two plots within a site were pooled for all analyses. Details of ant species composition are given elsewhere (Vanderwoude et al., submitted), and the analyses presented here are restricted to site comparisons of species richness, biogeographic profiles, and functional group composition.

Each species was described as having Eyrean (arid), Bassian (cool-temperate) or Torresian (tropical) affinities, or as being Widespread, according to the distribution of the species-group to which it belongs. Such designations were based on the second author's understanding of the biogeography of the Australian ant fauna, following and extending those published elsewhere (e.g. Andersen, 1993a; 1993b). Species were classified into functional groups according to their habitat requirements and competitive interactions, following Greenslade (1978) and Andersen (1990, 1995). These groups are: Dominant Dolichoderinae; Subordinate Camponotini; Hot, Cold, and Tropical climate specialists; Cryptic species; Opportunists; Generalised Myrmicinae; and Specialist Predators. Ant species richness and composition were compared across sites. The relative abundances of Dominant Dolichoderinae, Generalised Myrmicinae, and Opportunists were used to classify the ant communities of each plot following Andersen (1995) as a tool for exploring the possible impact of disturbance (fire) on community structure.

Results

A total of 88 species from 42 genera were recorded, with species richness being greatest at the annually burned site (74 species), least at the unburned site (43 species) and intermediate at the periodically burned site (63 species). These site differences were not simply artefacts of increased 'trappability' at burned sites following fire-induced habitat modification (Vanderwoude et al., submitted).

Most of the 88 species recorded represented either Widespread (40%) or Bassian (29%) taxa,

with 20% and 11% having Torresian and Eyrean affinities respectively. The relative abundance of Eyrean taxa was particularly high (36%), and that of Bassian taxa low (8%) at the annually burned site, with the reverse true for the unburned site (14% and 20% respectively; Fig. 1). Ants from Widespread species-groups dominated each site, with the relative abundance of this group inversely related to frequency of burning.

The most abundant functional groups were Generalised Myrmicinae (particularly species of *Pheidole* — 31% of total ants), Opportunists (particularly species of *Rhytidoponera* — 28%) and Dominant Dolichoderinae (species of *Iridomyrmex* — 27%). Together, these three groups accounted for 86% of total abundance and 41% of species richness. The relative abundances of functional groups varied markedly across sites (Fig. 2). The relative abundance of Dominant Dolichoderinae was positively related to fire frequency. Conversely, Opportunists comprised 65% of all ants at the unburned site, but only 16% at the annually burned site. Following Andersen (1995), ant community classifications at the annually burned, periodically burned, and unburned sites are DD3GM, DD2GM and DD1OPP respectively.

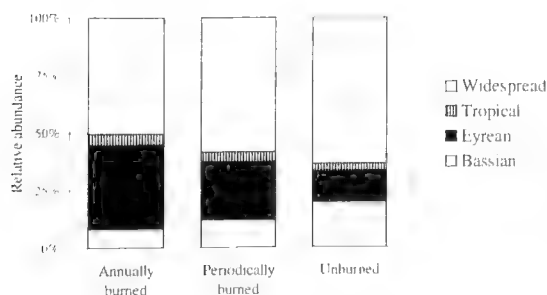


Figure 1 Relative abundance of ants from each biogeographical group.

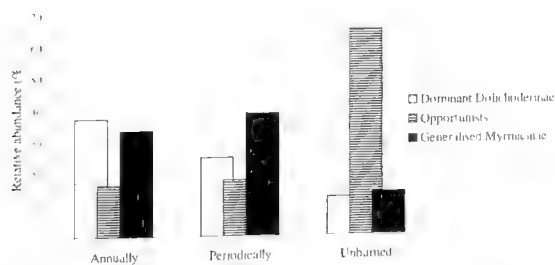


Figure 2 Relative abundance of the three major functional groups at each site.

Discussion

Ant community response to fire

Site species richness, biogeographical profiles, and functional group composition all varied systematically with fire frequency. With increasing fire frequency, species richness increased, the relative abundances of Eyrean taxa and Dominant Dolichoderinae increased, and the relative abundances of Bassian taxa and Opportunists decreased. Although the lack of treatment replication places constraints on the validity of attributing these site differences to the effects of fire, the differences in vegetation structure are known to be due to fire (Henry, 1961; Henry and Florence, 1966; House, 1995), and the above variation in ant community structure is consistent with these differences. In northern Australia, greatest ant diversity occurs in open (savanna) habitats, and the rainforest fauna is relatively depauperate (Taylor, 1972; Andersen and Majer, 1991; Andersen, 1992). Open habitats are dominated by species of *Iridomyrmex* (Dominant Dolichoderinae), many of which have Eyrean affinities (Andersen 1993b). Species of *Iridomyrmex* are commonly absent from heavily shaded habitats, where Opportunists are often the most abundant ants (Andersen and Majer, 1991; Andersen and Reichel, 1994; Reichel and Andersen, 1996), reflecting a lack of competition from behaviourally dominant ants.

These fire-habitat-ant relationships are reflected in the ant community classifications of each site. In a national context, DD2GM (periodically burned) and DD3GM (annually burned) communities are characteristic of open sites experiencing warm climates, whereas DD1OPP (unburnt) communities are characteristic of shady environments (Andersen, 1995).

The responses of ant communities to fire reported here parallel those recorded from savanna forests of monsoonal Australia (Andersen, 1991). Compared with unburned savanna, annually burned sites have higher species richness and a far greater abundance of *Iridomyrmex*, with sites burned every 2 years supporting intermediate communities. Annually burned savanna supported DD3GM communities (Andersen, 1995), as did the annually burned site in the present study. Unburned savanna supported DD1GM communities (Andersen, 1995), with Generalised Myrmicinae being the most abundant ants, rather than Opportunists as was the case in our unburnt site. We attribute this difference to the warmer climate, and

generally higher abundance of Generalised Myrmicines, of the monsoonal region.

Ants as bio-indicators in forestry management

Our study has shown that ant communities are sensitive to fire management practices in Bauple State Forest, thus satisfying one of the major criteria for selection of suitable indicator taxa. Importantly, we have also demonstrated that an effective ant-sampling program is a practicable option. Without any experience in invertebrate survey and systematics, one of us (the senior author) was able to run the sampling program and effectively sort specimens to species, after some initial training and further consultation with a specialist (the second author). Moreover, the use of functional groups within a general framework of community classification in relation to environmental stress and disturbance (Andersen, 1995), means that patterns of community composition could be interpreted without detailed knowledge of the biology of individual species.

In the future, we intend to test the suitability of using ant community responses to detect the more subtle impacts of forestry management practices. Using the results of the present study as baseline data, we have commenced an ant sampling program to monitor a replicated experiment involving the manipulation of fire and cattle grazing.

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References

- Andersen, A.N., 1983. Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology* 8: 127–137.
- Andersen, A.N., 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347–357.
- Andersen, A.N., 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica* 23: 575–585.
- Andersen, A.N., 1992. Regulation of 'momentary' diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *American Naturalist* 140: 401–420.
- Andersen, A.N., 1993a. Ants as indicators of restoration success at a uranium mine in tropical Australia. *Restoration Ecology* 1: 156–167.
- Andersen, A.N., 1993b. Ant communities of the Gulf region of Australia's semi-arid tropics: species composition, patterns of organization, and biogeography. *Australian Journal of Zoology* 41: 399–414.
- Andersen, A.N., 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* 22: 15–29.
- Andersen, A.N. and Majer, J.D., 1991. The structure and biogeography of rainforest ant communities in the Kimberley region of northwestern Australia. Pp 333–346 in: McKenzie, N.L., Johnston, R.B. and Kendrick, P.J. (eds), *Rainforests of Australia*. Surrey Beatty and Sons: Chipping Norton.
- Andersen, A.N. and Reichel, H., 1994. The ant (Hymenoptera: Formicidae) fauna of Holmes Jungle, a rainforest patch in the seasonal tropics of Australia's Northern Territory. *Journal of the Australian Entomological Society* 33: 153–158.
- Brown, A.G. and Turnbull, J.W., 1986. The Australian environment. Pp 11–27 in: Turnbull J.W. (ed.), *Multipurpose Australian Trees and Shrubs*. Australian Centre for International Agricultural Research: Canberra.
- Greenslade, P.J.M., 1973. Sampling ants with pitfall traps: digging-in effects. *Insectes Sociaux* 20: 343–353.
- Greenslade, P.J.M., 1978. Ants. Pp 109–113 in: Low, W.A. (ed.) *The physical and biological features of Kunoth Paddock in central Australia*. CSIRO Division of Land Resources Technical Paper No. 4, Canberra.
- Greenslade, J. and Greenslade, P., 1984. Invertebrates and environmental assessment. *Environmental Planning* 3: 13–15.
- Henry, N.B., 1961. Complete protection versus prescribed burning in the Maryborough hardwoods. *Queensland Forest Service Research Notes No. 13*: 1–13.
- Henry, N.B. and Florence, R.G., 1966. Establishment and development of regeneration in spotted gum-ironbark forests. *Australian Forestry* 30: 304–316.
- House, A.P.N., 1995. Fire ecology research in Queensland native forest — current status and new directions. Pp 86–97 in: Roberts, B.R. (ed.), *6th Queensland Fire Research Workshop*. Land Use Study Centre, University of Southern Queensland, Toowoomba.
- Majer, J.D., 1978. An improved pitfall trap for sampling ants and other epigeic invertebrates. *Journal of the Australian Entomological Society* 17: 261–262.
- Majer, J.D., 1983. Ants: bio-indicators of minesite rehabilitation, land-use and land conservation. *Environmental Management* 7: 375–383.
- Majer, J.D., 1984. Recolonisation by ants in rehabili-

- tated open-cut mines in northern Australia. *Reclamation and Revegetation Research* 2: 279–298.
- Majer, J.D., 1985. Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. *Australian Journal of Ecology* 10: 31–48.
- Neumann, F.G., 1992. Responses of foraging ant populations to high-intensity wildfire, salvage logging and natural regeneration processes in *Eucalyptus regnans* regrowth forest of the Victorian Central Highlands. *Australian Forestry* 55: 29–38.
- Noss, R.N., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4: 355–364.
- Oliver, I. and Beattie A.J., 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* 7: 562–568.
- Oliver, I. and Beattie A.J., 1996. Designing a cost-effective invertebrate survey: a test of some methods for the rapid assessment of invertebrate biodiversity. *Biological Applications* 6: 594–607.
- Reichel, H. and Andersen, A.N., in press 1996. The rainforest ant fauna of Australia's Northern Territory. *Australian Journal of Zoology* 44.
- Rosenberg, D.M., Danks, H.V. and Lehmkuhl, D.M., 1986. Importance of insects in environmental impact assessment. *Environmental Management* 10: 773–783.
- Southwood, T.R.E., 1978. *Ecological methods with particular reference to insect populations*. Chapman and Hall: London.
- Spellerberg, I.F., 1993. *Monitoring ecological change*. Cambridge University Press: Cambridge.
- Taylor, R.W., 1972. Biogeography of insects of New Guinea and Cape York Peninsula. Pp 213–230 in: Walker, D. (ed.), *Bridge and barrier: the natural and cultural history of Torres Strait*. Australian National University Press: Canberra.
- Vanderwoude, C., Andersen, A.N. and House, A.P.N., submitted. Community organization, biogeography and seasonality of ants in an open forest of south-eastern Queensland. *Australian Journal of Zoology*.
- Williams, K.S., 1993. Use of terrestrial arthropods to evaluate restored riparian woodlands. *Restoration Ecology* 1: 107–116.
- York, A., 1994. The long-term effects of fire on forest ant communities: management implications for the conservation of biodiversity. *Memoirs of the Queensland Museum* 36: 231–239.

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